Post-fledging begging and development in Southern Pied Babblers (*Turdoides bicolor*)

Alex Thompson

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

At the Percy FitzPatrick Institute of African Ornithology, Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

May 2013

Supervised by Professor Phil Hockey (deceased Jan 2013)

Co-supervised by Dr. Nichola Raihani, Associate Professor Peter Ryan (from Feb 2013)

Abstract

Elaborate solicitation displays are a common feature of care-giver-offspring interactions throughout the animal kingdom. These displays, termed begging, are seen to be the physical manifestation of parent-offspring conflict over provisioning. The environment that offspring find themselves in is likely to have consequences for the costs and benefits of begging behaviour, and thus the dynamics of begging. However, the overwhelming majority of empirical and theoretical studies have used nestling birds as their model system. Nestlings are stationary, in close proximity to their siblings, and broods tend to be provisioned by one adult at a time. Therefore, current understanding of begging dynamics has potentially been narrowed by studies of stationary offspring. There is however, a growing literature on the begging of offspring that are mobile, able to move between care-givers and provide constant begging signals. In this thesis I use fledgling Southern Pied Babblers (*Turdoides bicolor*) as a model system in which to investigate mobile offspring begging and the developmental consequences of post-fledging care. Firstly, I give a general background to the field and address the questions that can still be asked in Chapter 1. I then discuss the observational, experimental and analytical methods used throughout the study in Chapter 2. In Chapter 3, I investigate the structure of fledgling pied babbler begging calls. I show that like other mobile offspring, pied babblers have multiple begging call types that are used in different contexts. I also show that the structure and use of begging calls changes with hunger level, information that may be used by care-givers in provisioning decisions. Using a series of feeding and playback experiments, in Chapter 4, I explore the begging dynamics between fledgling pied babblers and care-givers. I show that fledgling begging is positively related to hunger, adult provisioning is positively related to begging and that fledgling begging is independent of the begging behaviour of siblings. I propose that the dispersed nature of the fledgling environment means that fledglings gain no provisioning benefits nor incur any provisioning costs from changes in their siblings begging. In Chapter 5, I use a novel approach to investigate Zahavi's blackmail hypothesis. I show that young fledglings face a trade-off: staying in the safety of trees or moving to the profitable yet risky ground to solicit care. Adults change their provisioning behaviour based on the risk that fledglings face, related to their location, and fledglings are thus able to gain more food by moving to riskier locations. In Chapter 6, I consider the long term consequences of fledgling behaviour during

dependence. Using natural observations and feeding experiments I disentangle the effects of initial advantages, investment in foraging and investment in offspring-adult associations on foraging development. I show that individuals who invest more in behaviours to promote individual-learning, foraging when young, develop relatively higher foraging efficiencies than their siblings. Finally in Chapter 7, I synthesize the finding of my thesis and relate these to current understanding in the field. In addition, I propose future work that could build on the research conducted in this study. The mobility of fledgling Southern Pied Babblers has led to the evolution of a care-giver-offspring interactions where offspring solicitation appears to signalling reliable signal of hunger, with the information contained within the structure of begging calls and fledgling's response to each other's begging revealing that begging is a way for individuals to signal their hunger. However, fledglings can still manipulate adults into provisioning them by threatening their own destruction.

Acknowledgments

This research was funded by the NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology and the British Ecological Society, under ethical clearance from the Science Faculty Animal Ethics Board, University of Cape Town (R2012/2006/V15/AR).

Firstly, I would like to thank my family. My parents always told me to pursue a career that I enjoyed and only put pressure on me to excel at whatever I chose to undertake. Without their sacrifices, support and encouragement I would not be doing what I am doing today. They have given me so much and there is no way I will ever be able to repay them in full or thank them enough. Thanks also to my brother, Morgan, for always bringing me back down to earth and also to his beautiful daughter Bella.

Secondly, thanks go to my supervisors. Phil Hockey and Nikki Raihani helped to guide me in my planning, preparations and write up. They helped me to hone my writing skills, and to restrict the number of tangents that I am prone to meander onto. They managed to do this whilst both going through major upheavals in their lives, and for the efforts during those trying times I will be forever grateful. I also thank Peter Ryan for stepping in after Phil's sudden death, you helped to steer me through the final choppy waters of UCT bureaucracy and streamline my writing at the very end .

Phil enabled me to pursue my dream of doing a PhD and of doing it on the study system that I really wanted to do it on, the babblers. His support has helped to change my life and I will be eternally grateful. His constant support has allowed me to follow my ideas, whilst reining me in when I become tangential. He was the heartbeat of the Fitz, its guiding light and its energy. He will be forever missed, but his legacy will live on.

Thanks to Tim Clutton-Brock and Marta Manser for allowing me to use the facilities at the Kuruman River Reserve and for their past support of the pied babbler project. Thanks also to Jamie Samson and Nate Thavarajah, for keeping the meerkat volunteers in check on the reserve and for the amusing radio chat. Joe Fenton and Melissa Delport helped out by keeping the 'friends' and Earthwatchers sufficiently occupied and out of our way at

Gannavlakte (GV). And finally, thanks to the meerkat volunteers for all of their radio calls that helped us find the babblers that little bit faster. It's also important to thank the De Bruins and Kotzes; I am sure they have no idea how much science is done on their land and how many papers they have been acknowledged in.

Sound analysis presented a horrible challenge during this PhD but I had help along the way from various people. Thanks to Simon Townsend for his patients while teaching me the fun world of pDFAs, I'll miss all of our silly Oxbridge jibes. Dave Humphries helped me out a lot during my brief stint at Macquarie, you introduced me to the scary world of Raven and helped out loads during field work at GV. Roger Mundry went above and beyond the call of duty by providing help to a poor PhD student drowning in R code on the other side of the world, many thanks.

Thanks to Matt Bell; who knew that a lowly 2nd year Natsci from Girton would still be asking for your help in formulating his scientific ideas 7 years later? And remember, Jesus rides a panda. I would also like to thank Amotz Zahavi for his comments on one of my chapters, interacting with him helped me to understand his thought processes more fully.

I have to thank my three field assistants: Fiona Finch, Adam Britton and John Forecast. Fiona, I am sorry that lugging that ladder around to all of those nests, in the middle of the Kalahari summer, has resulted in almost no data finishing up in this thesis. Legs, you were part of a legendary GV football team and provided good banter whilst in the field.

Time in the field wouldn't have been the same without the myriad of characters that traversed the poorly built and maintained stage of GV. We developed a strange pride for our corner of the reserve, climaxing in the unbeaten GV football team, with such esteemed members as Mike Finnie, Tom Flower, Matt Gribble, Dave Humphries, Mark Whiteside and Adam Britton. The girls offered a tonic to the comic machismo of the boys at GV, Lizzie and Tanya were always ready with quick one liners and a cup of tea/coffee and a piece of cake. Thanks to Boo for the Insanity. The Nelson-Flowers/Flower-Nelsons need a big thanks as well. Tom and Maple have given me advice throughout and helped keep the life history on the babblers ticking, and it's been fun to see Audry grow up in the Kalahari.

There are some people at the Fitz, without which this research would never have gotten off the ground. Hilary Buchanan, you are a magician, thanks for registering me every year and knowing the UCT system backwards and so allowing everything to seemingly flow smoothly. Thanks to Tania Jansen and Anthea Links, for putting up with my annoying receipts and requests, whilst providing endless stories of humorous family life and recipes for melk tert. Chris Tobler, thanks for being so forgiving about all of my equipment problems. Thanks also to Rob Little for all his help with wangling funding for me to go to conferences in far flung places. Margarett Koopman, you are as much an asset to the Fitz as the Niven itself, your tireless work allows us all to carry out our research that much easier, thank you.

I have had so much fun at the Fitz, there are a great bunch of people here. I have had some wonderful office mates during my time here. Thanks to Susie Cunningham for putting up with my stupid kiwi accent, I'm heaps beached az. Thanks to Rob Simmons for his four legged companions. Margaux Rat and Sophie Garcia-Heras, you provided some Gallic flair to our office. Other notable Fitzies were Tim Ried, Rowen Van Eeden, Chevonne Reynolds and Christine Moore. Jess I am sorry I didn't manage to finish at the same time as you.

I will miss Cape Town, it all started so wonderfully with two steaks at the Hussar with Rowan and Caroline Martin. And I will always remember the distinctly non-South African braais at Tim and Marie's house, lots of wine and French chocolate. It's a beautiful city and I will miss it dearly. Being away from home would have been far tougher had it not been for the Borgers, my second family. Laura, Klaus, Saskia and Max have made we welcome in Cape Town and let me tag along to many a Stormer's game at Newlands in the Whelan's box. Thanks so much for the welcome and kindness you have shown me.

Simon Griffiths provided me with the opportunity to spend a bit of time in Aussie at Macquarie University. It was nice to meet new people, such as Mia and Enrico, and enjoy a different atmosphere from the one at the Fitz. I also was able to spend some time at the Institute of Zoology in London, and again that helped to provide a fresh perspective on my work.

I also have to thank a bunch of guys who have no idea how much they have helped me, the FIFOs. The most enjoyable rugby team to play for, we play hard and have a jol! Without this time away from work I am sure my brain would have exploded. Thanks to the whole team and coaches for making me feel welcome but always reminding me that I am a pom!

Thank you to the CD drive in my desktop for reminding me of the importance of backing up, via self-immolation. There are three cars that have helped me get through this PhD: Paj, Percy, and Tazz. All those hours driving to Upington in Paj have made me love her, and Percy was the most fun to drive around the Kalahari. As for Tazz, no four-geared car should be able to do the things that you have done.

Finally, I have to thank Mandy. You are the person I would like to thank the most, without you none of this would have been possible. This PhD is as much yours as it is mine. All of the stress and strain that it has caused, all of the help and advice that you have given me, I can't thank you enough. You believe in me and I'm so grateful for that. You opened my eyes to the joy of the babblers, and often had to remind me that they are wild animals and are not deliberately trying to sabotage my research. And thanks to Kito for reminding me that there is more to life than work and science. Watching Kito grow up has been the most wonderful experience of my life.

I also need to thank the birds, for being so wonderful and enjoyable to work on. Fledgling babblers I would like to thank, in alphabetical order: Big Sam (BGSM), Big Tom (BGTM), Bahrain (BHRM), Blom (BLOM), Blossom (BLSM), Bumbag (BMBG), Bump (BMPP), Bobem (BOBM), Barmy (BRMY), Brom (BROM), Bum (BXMX), Chameleon (CHML), Column (CLLM), Camber (CMBR), Comic (COMC), Gobems (GBMS), Jamaica (GMCR), Gump (GMPP), Gemmell (GMYL), Gorm (GORM), Graham (GRHM), Girton (GRTM), Gimic (GYMC), Hobnob (HBMB), Gembok (HMBC), Hemghis (HMGS), Hemmingway (HMGY), L'Chaim (LHYM), Lil' Tim (LLTM), Lumber (LMBR), Lambert (LMBT), Limit (LYMT), Limey (LYMY), Mubble (MBBL), Mick (MCCC), McCoy (MCOY), Macpac (MCPC), McPoor (MCPR), Mugby (MGBY), Mohawk (MHWC), Milby (MLBY), Molt (MLTT), Mobel (MOBL), Moko (MOCO), Moot (MOOT), Moāri (MORY), Monty (MOTY), Mampoer (MPOR), Morepork (MRPC), Mirth (MRTH), Mortar (MRTR), Merit (MRYT), Mesquite (MSCT), Mount Gay (MTGY), Matapo (MTPO), Mc (MXCX),

Moxsy (MXSY), Meisie (MYCY), Mayhap (MYHP), Mizey (MYSY), Mater (MYTR), Omgel (OMGL), Omo (OMOO), Omph (OMPH), Piecemeal (PCML), Peckham (PCYM), Pygmalion (PGML), Plummet (PLMT), Pemble (PMBL), pumice (PMYS), Primal (PRML), Putmo (PTMO), Puma (PWMR), Rhyme (RHYM), Rollmop (RLMP), Rumba (RMBR), Roweyman (RWYM), Remus (RYMS), Scamp (SCMP), Shazam (SHSM), Slimmer (SLMR), Smuckle (SMCL), Smoo (SMOO), Smith (SMTH), Spammer (SPMR), Sesame (SSMY), Strum (STRM), Thomas (THMS), Thrum (THRM), Thyme (THYM), Tombliboo (TMLB), Tempo (TMPO), Tottenham (TOTM), Willem (WLLM), Wimpy (WMPY), Wotmo (WTMO), Xixmix (XXMX), Waimate (YMTY) and Yesmax (YSMX).

Authors' Declaration

I declare that this thesis is the result of my own research and, except where indicated by specific reference in the text, contains no work in collaboration with others. The text does not exceed 80,000 words. I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes. No part of this thesis has been submitted to any other university in application for a higher degree. Any views expressed in this thesis are those of the author.

Signed: Date:

Papers arising from this thesis

The following manuscript has been accepted for publication prior to the submission of this thesis. This manuscript has multiple authors, each of which contributed in some way to its production. Dr Ridley and I came up with the idea, my supervisors Dr Raihani and Prof. Hockey assisted in revisions to the manuscript, and Mr Britton and Ms Finch assisted with field work. Contributions: Thompson 70%, Ridley 20%, Raihani 4%, Hockey 4%, Britton 1%, Finch 1%.

Thompson, A.M., Raihani, N.J., Hockey, P.A.R., Britton, A., Finch, F.M. & Ridley, A.R. (2013) The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. *Proceedings of the Royal Society of London Series B - Biological Sciences* **280**, 20130558

After the submission of this thesis for examination and before the return of the examiners reports an additional manuscript was accepted for publication.

Thompson, A.M., Ridley, A.R., Hockey, P.A.R., Finch, F.M., Britton, A. & Raihani, N.J. (2013) The influence of siblings on begging behaviour. *Animal Behaviour* **86**, 811-819

Table of Contents

Chapter 1

Introduction

Introduction

1.1 Parent-offspring interactions

The majority of species exhibit no parental care beyond their initial investment in the production of offspring (Smiseth et al. 2012) and, as such, many parents have limited scope for interacting with their offspring. However, many animal species have evolved forms of parental care that continue post birth or hatching (reviewed in Smiseth et al. 2012). These forms of parental care give parents and offspring the opportunity to interact repeatedly over a period of time. Parents may simply be a source of food, warmth or protection for dependent offspring. Alternatively, in addition to providing food to offspring parents may also be a source of information (Midford et al. 2000; Platzen & Magrath 2004; Allen & Clarke 2005). Parents may provide offspring with information with short-term value, such as the predation risk in the environment (Magrath et al. 2007). Offspring may also gain information that could benefit them in the long-term, such as the information about the location of optimal foraging microhabitats, what to eat and techniques to extract food (Terkel 1996; Langen 2000; Galef & Giraldeau 2001; Thornton & Hodge 2008). Offspring will benefit from interactions with their parents if they obtain resources or gain information that improves their survival and reproductive prospects.

Prior to Trivers (1974), the prevailing idea was of the family being a harmonious unit. Parent-offspring interactions were broadly expected to be beneficial for both parties, as offspring gain protection from predators and parasites, as well as nutritional benefits and potential learnt benefits from parental care, and parents gain reproductive success (Tallamy & Denno 1981; Knouft et al. 2003; Thornton & McAuliffe 2006; Smiseth et al. 2012). However, there may be conflicts between offspring and parents over the optimal level of resources which should be invested. The conflicts are based around the ideas Hamilton (1963, 1964) put forward to explain altruistic and cooperative behaviour, with Trivers (1974) expanding on these to propose his theory of parent-offspring conflict (POC). Due to the genetic asymmetries created by sexual reproduction, parents and their offspring will disagree over the optimal level of investment. All else being equal, as parents are equally

related to all of their offspring, they will do best to spread their resources equally between their offspring over their reproductive life-time. Conversely, offspring are twice as related to themselves as they are to their parents or siblings. Offspring will do best if they monopolize current parental resources at the expense of their current and future siblings, until the point that the cost they impose on their siblings is twice that of the benefit they gain from additional investment. As such, parents and offspring are expected to disagree over the optimal level of parental investment with offspring preferring to receive more than parents want to give. Inherent in this theory is not just a conflict between parents and offspring but also a conflict between siblings over access to resources. POC theory has been used to explain the existence of a wide variety of familial behaviours such as siblicide (Mock 1987; Mock & Parker 1998) and infanticide (O'Connor 1978), and to understand negotiation within families (Johnstone & Roulin 2003; Hinde 2006; Hinde & Kilner 2007). These conflicts are more likely to occur in the context of provisioning than information use, with the begging of dependent young being seen to be the physical manifestation of POC (Smiseth et al. 2008). This is because provisioning inherently imposes costs, as food given to one individual cannot be given to another, and once fed to offspring it cannot be consumed by the care-giver. In contrast, the passive transfer of information has few, if any, costs and can flow between multiple individuals simultaneously (Nicol 2006).

1.2 Care-givers as a source of food

Parental care can take many forms, from thermoregulation to protection from predators, but one of the most conspicuous aspects is the direct provisioning of food to offspring (Smiseth et al. 2012). Not all offspring are cared for by their genetic parents, with some species exhibiting high rates of extra-pair paternity (Gerlach et al. 2012), egg dumping (Tallamy 1985), brood parasitism (Davies et al. 2003) or more social forms of breeding (Stacey & Koenig 1990). Therefore, care-givers may be a more useful term to apply to provisioning adults. Offspring in many vertebrate and invertebrate species exhibit exaggerated solicitation displays to gain food from care-givers. These displays involve signalling between offspring and their care-givers and can take many forms (Kilner 1997; Rauter & Moore 1999; Saino et al. 2000; Tanaka & Ueda 2005; den Boer & Duchateau 2006). Solicitation displays can be complex, with multiple signalling components that can convey different information or act as back up signals (Møller & Pomiankowski 1993; Kilner 1995;

Johnstone 1996a). Begging theory typically posits that an offspring's begging investment is a signal of its need, being defined as the 'increase in an offspring's personal fitness resulting from receipt of a unit of food' (Royle et al. 2002). However, due to the difficulty of empirically measuring long-term fitness consequences, it is almost impossible to accurately quantify need (Mock et al. 2011). Instead, hunger has been used as a proxy to measure short-term need, although this too has its problems due to the fact that provisioning individuals at the extremes of condition may have little or no effect on their future reproduction regardless of their hunger level (reviewed in Mock et al. 2011). However, Johnstone & Kilner (2011) argue that there is no reason to treat signals of short-term need differently from those of long-term need, as theory makes no distinction between the two.

To ensure that begging signals do not escalate and are reliable there needs to be a cost to their production (Zahavi 1975; Zahavi 1977a). Reliable signals correlate with and accurately convey cryptic information to receivers (Kilner 2002a). This concept, that begging and provisioning behaviour are contingent upon these behaviours being costly, has been crucial in the understanding of the evolution of begging signals (Grafen 1990; Godfray 1991; Johnstone & Grafen 1992; Godfray 1995). Investigations into the cost of begging call production have focused mainly on two costs: energetic and predation. Studies seeking to determine whether begging carries significant energetic costs have been inconclusive, for example Leech & Leonard (1996) found evidence for an energetic cost, whereas McCarty's (1996) results seemed to suggest that begging carried a minimal metabolic cost. In contrast, empirical investigations have tended to show predation risk to be a significant cost to vocal begging, at least in nestling broods (Haskell 1994; Leech & Leonard 1997; Haskell 1999; McDonald et al. 2009). All elements of interactions between care-givers and offspring interactions incur direct costs or produce direct benefits, with care-givers benefiting from the survival of current offspring when provisioning them but simultaneously paying potential costs to their own survival and future reproduction (Nur 1988; Monaghan & Nager 1997). In addition, due to the genetic relatedness within families, individuals will suffer indirect costs or indirect benefits from all provisioning events (Hamilton 1964; Trivers 1974). All of these costs and benefits affect an individual's life-time reproductive success, and it is very difficult to truly measure these in the natural world (Mock & Forbes 1992; Mock et al. 2011).

In species with single offspring, begging intensity may often accurately reflect current hunger levels, as they cannot directly compete for provisioning with their future siblings (Godfray 1991). However, in species with multiple dependent young there is the potential for begging to be influenced not only by internal state but also by the need and begging effort of rivals (Godfray 1995). Investigating how offspring respond to each other's begging behaviour is a key step in understanding whether begging influences the allocation of resources or the total amount of food delivered (Johnstone 2004).

1.3 Care-giver response to begging

Care-givers who are insensitive to offspring need are ineffective at provisioning, resulting in the production of lower quality offspring (Grodzinski & Lotem 2007). Thus, care-givers are expected to respond to increased begging with increased provisioning, although there are notable exceptions (Kölliker et al. 2000; Thorogood et al. 2011). How care-givers respond to offspring begging depends on who controls the allocation of food (Parker et al. 2002). The two main theories to explain the allocation of provisioning are honest signalling and scramble competition, with the key difference between them being whether offspring or care-givers control provisioning (Parker et al. 2002; Royle et al. 2002). Honest signalling proposes that care-givers actively choose which offspring to provision and requires care-givers to be able to discount the effects of offspring's competitive abilities on their begging signal and provision the individuals with greatest need (Godfray 1995; Royle et al. 2002). Conversely, care-givers are passive under models of scramble competition and provision the individual with the most extreme signal (Rodríguez-Gironés et al. 2001; Parker et al. 2002; Royle et al. 2002). In addition, scramble competition occurs when adults allocate a fixed amount of resources. Both theories have similar predictions, with begging intensity reflecting need and provisioning being related to begging intensity (Royle et al. 2002). The provisioning response of care-givers can manifest itself in different ways, they may increase provisioning to the target offspring while reducing provisioning to the rest of the brood, or alternatively they could increase total provisioning levels to the brood (Johnstone 2004). In this way, care-giver response to begging can influence how offspring respond to their siblings' begging behaviour, as it influences the level of care that offspring receive.

Interactions between offspring and care-givers are not static over the period of dependence, as offspring develop and the environmental conditions vary. Care-giver response to begging may be context dependent, with offspring begging in situations of higher risk potentially eliciting more provisioning (Zahavi 1977b; Johnstone 1996b; Lummaa et al. 1998). In addition, environmental factors may influence care-giver ability to respond to increased offspring demand, with care-givers responding less when conditions are poor (Thorogood et al. 2011; Kilner & Hinde 2012). Control over provisioning is also likely to lie on a continuum and vary with offspring age (Royle et al. 2002). The reliability of signals may also show ontogenic shifts. For example, mouth colour in canaries (*Serinus canaria*) is a reliable signal of hunger when offspring are young but ceases to be reliable as they get older (Kilner 1997). However, the current theoretical models used to describe begging behaviour do not take into account these dynamic aspects of the dependent phase (Godfray & Johnstone 2000; Royle et al. 2002). These models do not consider the repeated interactions that occur between care-givers and offspring, nor the changes in offspring ability to control the allocation of resources (Godfray & Johnstone 2000; Royle et al. 2002). These dynamic aspects of development are likely to have strong effects on the optimal behaviours of care-givers and offspring. Empirical investigations of offspring in different environmental contexts and at different developmental stages may help theorists to model the dynamic nature of these interactions more fully.

1.4 Honest vs dishonest signals

Honest signalling theory posits a 1:1 relationship between offspring begging intensity and offspring need, enabling the receiver to optimally allocate resources to the offspring in most need of them (Royle et al. 2002). Under honest signalling, care-givers are expected to provision offspring in relation to their begging because fitness returns to care-givers are correlated with begging level (Roulin 2002). Offspring begging signals that are not directly proportional to need (e.g. escalated signals) will misrepresent an individual's need and can thus be considered dishonest. Signalling theory predicts that dishonest signals will not persist (Grafen 1990; Godfray 1995), but these theories require signalling to carry a cost (Godfray 1995). However, low levels of dishonesty may be evolutionarily stable and signals only need to be honest on average to ensure a stable signalling system (Johnstone & Grafen 1993).

Begging can be 'honest' under honest signalling and scramble competition models (Royle et al. 2004), with begging always being 'honest' under honest signalling and being 'honest' depending on the context for scramble competition (Royle et al. 2002). The two models do differ on how offspring are expected to respond to each other, with scramble competition predicting the escalation of begging, while honest signalling predicts no begging escalation (Royle et al. 2002).

Typically, empirical investigations that find a positive relationship between offspring hunger and begging effort interpret their results as providing evidence for begging being an honest signal of offspring need (Rauter & Moore 1999; Villaseñor & Drummond 2007; Marques et al. 2009). However, in situations such as those that occur with parasitic species like Eurasian cuckoos (*Cuculus canorus*), begging may reliably reflect need, with hungrier chicks begging more. This would not be considered an honest signal, however, as host-parents are not responding optimally due to cuckoo chicks not being their offspring (Kilner et al. 1999). In addition, an understanding of the life-time benefit that a unit of food will give to an individual is required to determine an individuals need (Godfray 1991; Mock & Forbes 1992). In many long-lived species this is difficult to empirically calculate, thus it is not possible to determine if begging has a 1:1 relationship with need. It may be more useful to consider any begging signals that correlate with short-term hunger to be 'reliable' signals, rather than using the term 'honest'.

1.5 Empirical investigation into begging

Many studies have been conducted to investigate begging behaviour in a variety of species in multiple taxa (Weygoldt 1980; Kilner et al. 1999; Kaptein et al. 2005; den Boer & Duchateau 2006; reviewed in Mock et al. 2011). However, the overwhelming majority of studies have been carried out on altricial nestling birds (Trillmich & Wolf 2007; Kunc et al. 2007). The environment that nestlings inhabit is broadly similar across most avian species: confined to one physical location, typically in close proximity to siblings and separate from foraging adults. Offspring in other taxa, species or even at different periods of avian development, experience a different environment to that of altricial nestlings, often being

mobile, dispersed and close to provisioners (McGowan & Woolfenden 1990; Rendell & Whitehead 2001; Smiseth et al. 2003; Gilchrist 2004). Begging behaviour is influenced by costs and benefits, and limiting investigations to one period of development reduces our understanding of how these change. The post-fledgling phase of avian development is understudied, perhaps due to the difficulties in observing and manipulating fledglings (McGowan & Woolfenden 1990; Sankamethawee et al. 2009; Shizuka & Lyon 2013). By investigating begging in fledglings, who like the young of many other species are mobile and dispersed (Manser & Avey 2000; Gilchrist 2004), a greater understanding of the factors affecting begging behaviour can be gained.

The environments that mobile and stationary offspring experience are qualitatively different, with implications for provisioning and signalling behaviour. Three factors may play important roles in shaping begging in systems with mobile offspring. First, in stationary systems, such as those of nestling birds, communication between offspring and care-givers is typically restricted to feeding events (Manser & Avey 2000). When offspring are mobile and can follow adults, there is the potential for continuous signalling to occur. Resource allocation may be different in mobile systems due to adults potentially receiving greater levels of information. Second, freely mobile offspring can beg in multiple contexts, while following foraging adults, while self-foraging and when adults have found a food item (Kunc et al. 2007). Mobile offspring can actively solicit care by moving directly towards foraging adults and following them (Gilchrist 2004; Hodge et al. 2007). In contrast, begging by stationary offspring is typically restricted to only one context: when adults have arrived to provision the litter or brood (Leonard & Horn 2001a; but see Roulin et al. 2000). As a result, the begging calls of mobile offspring may be used in different ways from those of stationary offspring (Kunc et al. 2007). Third, direct physical competition between nestlings often determines the allocation of resources at feeding events, because provisioning care-givers typically feed the closest offspring (Rydén & Bengtsson 1980; Smith & Montgomerie 1991; Kacelnik et al. 1995; Kilner 2002b). Asymmetries in physical competitive ability have the potential to play a major role in the allocation of food in such stationary systems. However, in mobile systems weaker offspring can move away from stronger competitors, beg to a different care-giver and thus may be able to reduce the impact of physical asymmetries.

Therefore, the begging strategies used by mobile offspring may be different to those of stationary offspring.

1.6 Cooperative breeding

Cooperative breeding occurs when parents receive assistance from other individuals in the production of young (Stacey & Koenig 1990). In some cases, individuals forego their own reproductive attempts in order to assist the reproductive attempts of other individuals (Stacey & Koenig 1990). Therefore, cooperative breeding poses a deep question to evolutionary theory: with natural selection favouring those individuals who maximize the number of surviving offspring they produce (Darwin 1859), how can this apparently altruistic behaviour evolve? This has led to many long-term studies being established to understand the evolutionary processes that drive the development and maintenance of cooperation (Koenig 1981; McGowan & Woolfenden 1990; Stacey & Koenig 1990; Balshine et al. 2001; MacGregor & Cockburn 2002; Gilchrist 2004; Hodge et al. 2007; Ridley & Huyvaert 2007). In most cooperatively breeding vertebrates, groups form due to the delayed dispersal of offspring (Cant 2012). Individuals can increase their inclusive fitness by helping in the reproductive attempts of related individuals (Hamilton 1963; Hamilton 1964), and recent comparative analysis supports this as a driver for the evolution of cooperative breeding (Cornwallis et al. 2010; Lukas & Clutton-Brock 2012). Individuals can accrue this indirect fitness by enabling relatives to produce more offspring than they would on their own, by reducing the interval between breeding attempts (Ridley & Raihani 2008) or increasing offspring survival (Emlen 1991). Unrelated individuals can gain direct benefits from helping, such as enhanced survival, enhanced likelihood of becoming a breeder and increased fecundity on becoming a breeder (reviewed in Emlen 1991).

1.7 Extended care

Cooperative breeding species typically have prolonged periods of offspring care, relative to biparental or uniparental species (Langen 2000). However, the duration of care can be highly variable within species (Stacey & Koenig 1990; Ridley & Raihani 2007a). Parental care provides obvious short-term benefits to offspring, through nutritional provisioning and protection from predators (Alonso-Alvarez & Velando 2012). Prolonged care can have long-term life-history consequences for offspring as it provides the opportunity for information

transfer between care-givers and offspring and time for offspring to learn and develop their skills and behaviours in a relatively safe environment (Langen 1996a; Thornton & McAuliffe 2006; Thornton 2008a; Hoppitt et al. 2008). The long-term benefits of prolonged care (Lindström 1999; Ridley & Raihani 2007a) make it likely that offspring have evolved behaviours to maximize their foraging ability and condition when the duration of care they receive can be variable.

1.8 Begging in a cooperative breeder

Cooperative breeders offer three main advantages in the study of begging dynamics. First, cooperative breeders tend to have prolonged periods of offspring care (Langen 2000), providing an ideal situation in which to investigate begging behaviour during different periods of offspring development. In avian species this allows the study of begging throughout the whole period of offspring development and not just of nestlings. Second, cooperative species have varying numbers of helpers to provision dependent young. The presence of helpers has the potential to reduce the cost of care through load-lightening (reviewed in Emlen 1991) and may accordingly influence the overall care available for offspring and therefore the level of competition over care (MacNair & Parker 1979; Godfray 1995; Rodríguez-Gironés 1999; Romano et al. 2012). Care from helpers has the potential to be additive (Mumme 1992; Valencia et al. 2006; Russell et al. 2007b), with parents maintaining their level of care and every extra helper adding to the overall level of care provided to offspring. Helper care can also be compensatory (Brown et al. 1978; Hatchwell 1999; Russell et al. 2007a; Meade et al. 2010), where parents reduce their investment in the presence of helpers. Finally, once the offspring of cooperative breeders have left the nest or den they continue to beg and remain dependent while following the group (Gilchrist 2004; Hodge et al. 2007; Thompson & Ridley 2013). Therefore, cooperative breeders provide an ideal opportunity to investigate offspring begging and adult provisioning strategies in a mobile system. Considering the social and environmental context in which begging occurs is crucial in understanding the processes behind the behaviour (Kedar et al. 2000; Royle et al. 2002). Therefore, investigations into the begging dynamics of cooperative species will enable a broader understanding of the mechanisms that govern offspring-care-giver communication and POC.

1.9 Care-givers as a source of information

Parents and care-givers are able to provide offspring with a wide range of information, from the environmental conditions they will experience post-hatching (Hinde et al. 2009) to the presence of predators (Suzuki 2011). Information transfer can take a variety of forms, from passive forms of social-learning such as local enhancement and public information (Giraldeau & Templeton 1991; Danchin et al. 2004) to instances where one individual actively teaches another (Franks & Richardson 2006; Thornton & McAuliffe 2006; Raihani & Ridley 2008). In addition to social learning, offspring may learn skills via trial-and-error and practice (Spence 1936; Laland & Plotkin 1992; Thornton 2008b). Individual-learning improves motor skills and neural development and leads to gradual improvement in behaviours.

Care-givers may provide information that benefits offspring in the short-term, such as changes to the local predation risk (Davies et al. 2004; Platzen & Magrath 2005), or in the long-term, such as song development or mate choice (Bereczkei et al. 2004; Beecher & Burt 2004; Greig et al. 2012). Care-givers might also help offspring develop foraging skills, by providing information about how to extract food (Terkel 1996) or the location of optimal foraging patches (Thornton & Hodge 2008). Individuals typically develop their foraging skills over the course of their dependent period, so that they are proficient enough to meet their energy requirements upon independence (Heinsohn 1991; Langen 1996b; Yoerg 1998). Investigating foraging development in cooperative breeders will expand current understanding of the role of individual and social-learning in development.

1.10 Pied babblers

I used Southern Pied Babblers *Turdoides bicolor* (hereafter referred to as pied babblers) as a model system to investigate offspring begging and development. Pied babblers are medium sized (~75g), cooperative breeding passerines, with prolonged post-fledgling care (Ridley & Raihani 2007a), that forage terrestrially in open habitats and range through the semi-arid savannahs of the Kalahari basin and adjacent areas (Hockey et al. 2005). Pied babbler groups consist of a dominant pair with a varying number of subordinates, who help to provision dependent young and maintain a year-round territory (Ridley & Raihani 2007b; Raihani & Ridley 2007a; Golabek et al. 2012). After fledging, offspring accompany the

foraging group and remain dependent on provisioning from all group members for up to 97 days (Ridley & Raihani 2007a). Pied babbler fledglings use a mobile begging system, similar to that of other cooperatively breeding species (Hodge et al. 2007), to solicit care from foraging adults (Thompson & Ridley 2013). Therefore, these birds offer an ideal study species for investigating begging and development in mobile offspring. The population of pied babblers that I studied is habituated to close human observation and amenable to experimental manipulation, in particular supplemental feeding and vocal playbacks (Radford & Ridley 2006; Bell et al. 2010; Thompson & Ridley 2013). This ability to experimentally manipulate offspring and care-givers is crucial to understanding the dynamics of begging in any provisioning system (Johnstone 1996b; Kölliker 2003). Studying pied babblers allows investigation into the begging system of a cooperatively breeding species when the majority of empirical studies investigating have begging have focused on uni or biparental species (Price & Ydenberg 1995; Weary & Fraser 1995; Smiseth et al. 2003). The long period of dependence that pied babbler fledglings go through, coupled with the fact that adults have been shown to teach offspring (Raihani & Ridley 2008a) and use specific calls to attract them to divisible food patches (Radford & Ridley 2006), means that pied babblers are an ideal species in which to investigate foraging development.

1.11 Thesis structure

In this thesis I investigate the dynamics of solicitation and foraging development in fledgling pied babblers. Using natural observations and experiments I investigate the interactions between care-givers and fledglings. I aim to answer a series of questions:

1. How does hunger affect begging?
2. How does begging change with age?
3. Is there a sex difference in begging calls?
4. Are begging calls individually identifiable?
5. How do care-givers respond to begging?
6. How do fledglings respond to the begging of their brood mates?
7. What role does predation risk play in fledgling solicitation?
8. What factors are most important in influencing foraging development?

In Chapter 2, I begin with a description of the ecology of pied babblers, the study site and population, and the data collection and analytical methods used in this thesis. Chapter 3 examines the structure and function of fledgling begging calls, investigating the information contained in fledgling begging calls and the context in which they are used. In Chapter 4, I investigate the factors affecting fledgling investment in begging and adult responses to begging behaviour. This chapter uses feeding and playback experiments to determine how hunger and sibling behaviour influence begging in fledgling pied babblers and seeks to understand how the fledgling environment shapes these behaviours. Chapter 5 provides experimental evidence that fledgling pied babblers can use predation risk to blackmail care-givers into increasing their feeding rate. Chapter 6 evaluates the importance of initial advantages, investment in foraging and investment in offspring-adult associations in shaping the development of foraging skills in pied babblers. In Chapter 7, I synthesize the results of this thesis and discuss their implications and contributions to the study of offspring begging and development.

Chapter 2

General methods and materials

General methods and materials

2.1 Study site

2.1.1 *Kuruman River Reserve*

This study was conducted at the Pied Babbler Project (established 2003) in the Southern Kalahari at the Kuruman River Reserve (KRR), Northern Cape, South Africa (26.58°S, 21.49°E)(Figure 2.1). The reserve covers an area of 3,500 ha, approximately 6.8km long by 5.3km wide. The reserve is uncultivated former ranch land. Since 2001 all stock animals have been removed and native antelope reintroduced. These include eland (*Taurotragus oryx*), red hartebeest (*Alcelaphus caama*), wildebeest (*Connochaetes taurinus*), springbok (*Antidorcus marsupialis*) and gemsbok (*Oryx gazelle*). Other research conducted at the reserve investigates the behavioural ecology of meerkats (*Suricata suricatta*), yellow mongooses (*Cynictis penicillata*) slender mongooses (*Galerella sanguinea*), fork-tailed drongos (*Dicrurus adsimilis*), yellow-billed hornbills (*Tockus leucomelas*) and crimson-breasted shrikes (*Laniarius atrococcineus*).

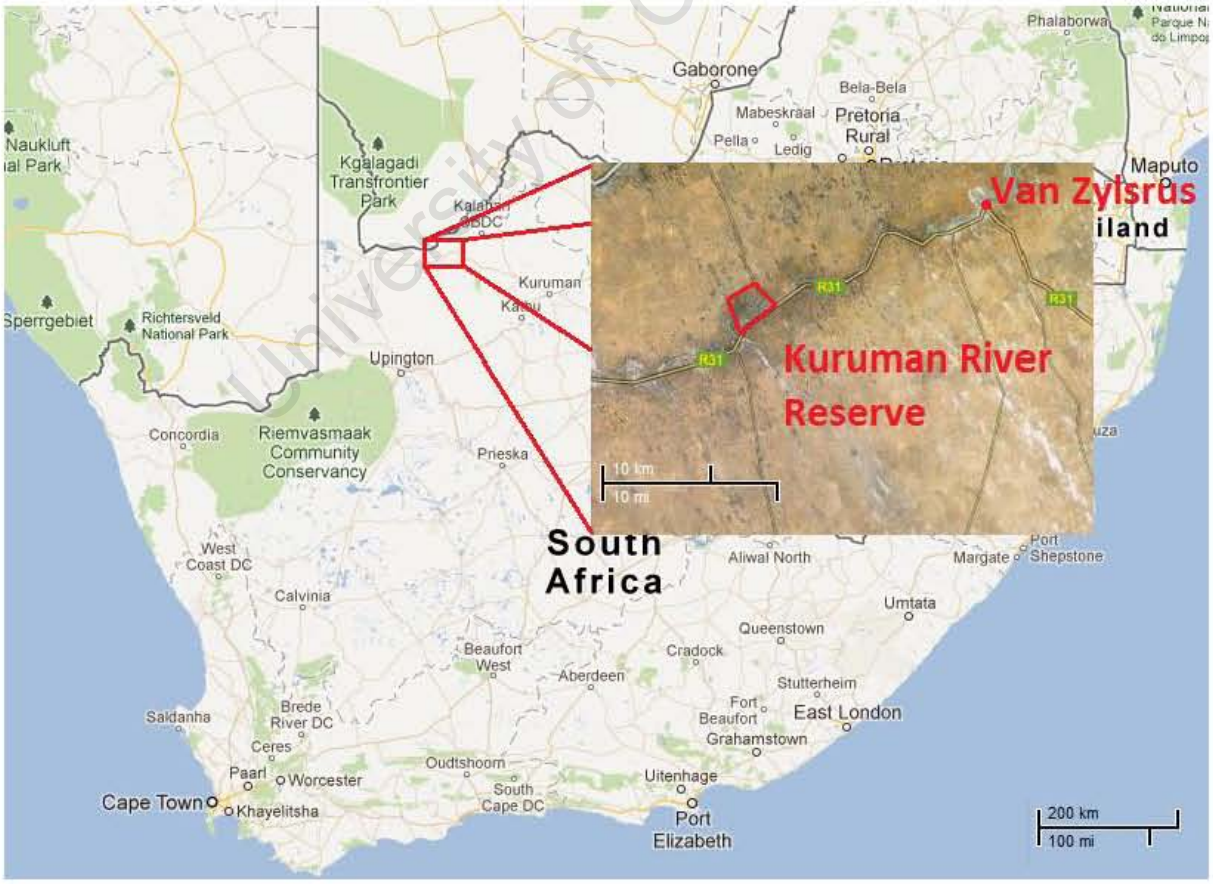

Figure 2.1 Location of the study site, Kuruman River Reserve, in South Africa.

2.1.2 *Habitat*

The reserve comprises five main habitat zones (Ridley & Thompson 2011). A dry riverbed, the Kuruman River, runs through the reserve, its flora consists of tall *Acacia erioloba* (approximately 11 m in height) and large *Ziziphus mucronata* (approximately 8 m in height) and after summer rain it is covered in various annual grasses and angiosperms. Away from the riverbed, the habitat becomes a mixture of tall, long sand dunes supporting a variety of tree species along their ridges; *Acacia erioloba*, *Acacia mellifera*, *Grewia flava*, and *Boscia albitrunca*. In some areas of the dune systems dense thickets of *Acacia mellifera* form, these can be up to 100 m^2 in area. The valleys between the dunes often contain large flats, 40-150 m wide, dominated by *Rhigozum trichotomum*, with perennial shrubs and annual grasses. Furthest away from the riverbed the habitat is dominated by low undulating dunes with small *Acacia haematoxlyon* (~3m in height) and thick clumps of tall perennial grasses. In years with heavy rain large areas of the reserve, particularly the dunes and flats, become dominated by swathes of *Schmidtia kalihariensis* (up to 1.2 m in height).

2.1.3 *Climate*

The habitat is semi-arid, with a mean annual rainfall of 326 mm (1997-2012). During my study the mean annual rainfall was 457 mm (2009-2012). The year is split in to two main seasons (see Figure 2.2); cool and dry winter (May-September) and a hot and wet summer (October-April) (Raihani & Ridley 2007a). Rainfall is unpredictable and typically occurs in heavy storms. Rainfall (mm) was measured at the study site using a standard rain gauge.

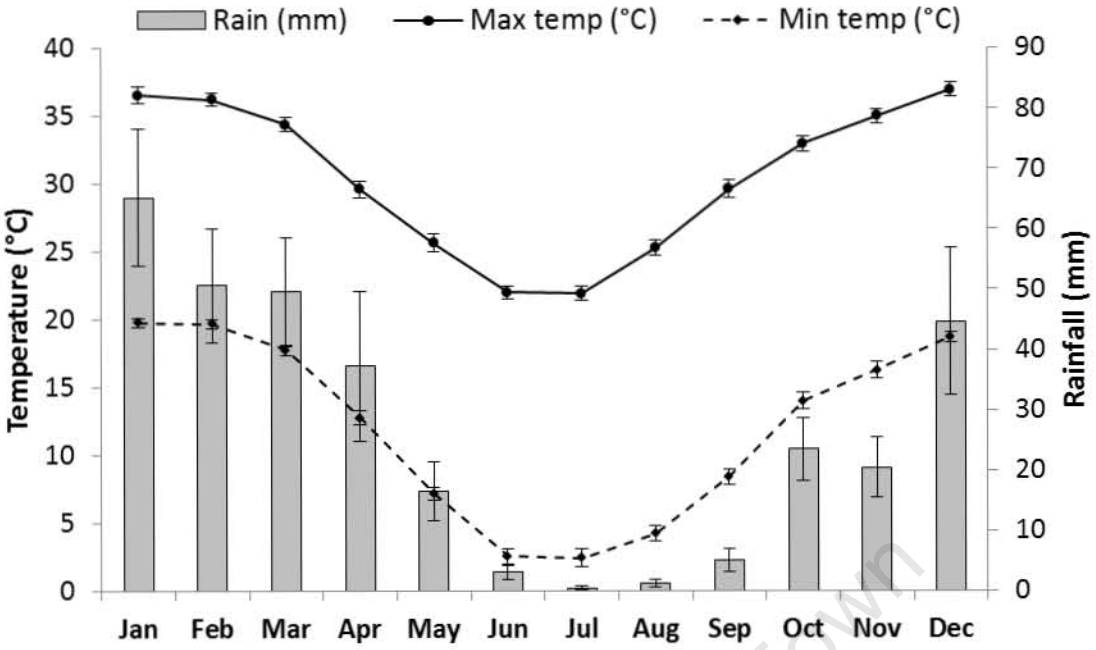

Figure 2.2 KRR annual temperature and rainfall. Mean maximum and minimum monthly temperature (°C ± S.E.) and mean monthly rainfall (mm ± S.E.). Data are from 2006-2012.

2.2 Study species

2.2.1 *Description and distribution*

Pied babblers are medium sized (70-95 g), cooperatively breeding passerines. They are members of the family Timaliidae (Old World babblers). Their conservation status is listed as 'Least Concern' in accordance with the IUCN 3.1 red list (Bird Life International 2013). Pied babblers have a large distribution that covers the semi-arid areas of Southern Africa, including parts of Namibia, Botswana, Zimbabwe and South Africa (Hockey et al. 2005).

2.2.2 *Social system*

Pied babblers live in stable groups that inhabit and defend a year round territory (Golabek et al. 2012). The groups are structured with a dominant breeding pair, who monopolise the breeding (ca 95% of offspring are sired by the breeding pair (Nelson-Flower et al. 2011)), and subordinate non-breeding helpers. Dominant individuals are identified by frequent aggressive behaviours (pecking and other attacks) towards other group members, extended preening bouts together and through greater investment in incubation and nest building. Groups are highly kin-structured, with subordinates typically being retained offspring of the breeding pair. However, subordinates can also be the siblings of dominant individuals or

unrelated immigrants. All members of the group help to raise the young, with contributions to incubation, brooding and provisioning to both nestlings and fledglings (Raihani & Ridley 2007a; Ridley & Raihani 2008). However, overnight incubation and brooding is only ever carried out by the dominant female. The other non-breeding related cooperative behaviour that is most obvious is sentinel activity, with birds taking it in turns to forego their own foraging and act as a look-out for the group (Ridley & Raihani 2007a; Hollén et al. 2008; Bell et al. 2010; Ridley et al. 2013). To attain a dominant breeding position both sexes can either inherit a breeding position, relatively rare, or disperse to a non-natal group (Raihani et al. 2010; Nelson-Flower et al. 2012). However, males are more likely to inherit breeding positions, whereas females are more likely to oust a resident breeder and as such females are more likely to disperse voluntarily while males are more likely to be evicted (Raihani et al. 2010).

2.2.3 *Breeding and care*

Pied babblers either build their own open cup nests or use abandoned wattled starling *Creatophora cinerea* nests (Ridley & Thompson 2011), laying 2-5 eggs (usually one each day). The eggs are incubated for 13-15 days, and the mean brood size is 2.03 ± 0.14 nestlings S.E. (range 1-4) (Ridley & Raihani 2007b). Nestlings remain in the nest for 13-18 days, with larger groups retaining young in the nest for longer before fledging (Raihani & Ridley 2007b). The breeding period extends from October-March (Ridley & Thompson 2011), during which time groups can have up to 3 (mean: 1.25 ± 0.15 S.E.) successful breeding attempts (Ridley & Raihani 2008). Pied babblers fledge when they are still relatively underdeveloped and for the first few days are unable to fly and are poorly mobile (Ridley & Raihani 2007b). Fledglings are provisioned for up to 97 days (Ridley & Raihani 2007b), until they have developed sufficiently competent foraging skills. Whilst dependent upon adult care-givers, pied babbler fledglings beg vigorously and follow individual adults closely (Figure 2.3), a behaviour termed 'social-foraging' in Thompson & Ridley (2013) but for clarity in this thesis I use the term 'association'. Associations can vary in duration and occur throughout the dependent period. Aggression towards fledglings increases as they reach independence (Raihani & Ridley 2008b) and competition between fledglings, manifest through aggressive interactions, is common and has been shown to occur more with female chicks (Raihani et al. 2008).

Figure 2.3 An adult care-giver provisioning a begging, dependant fledgling.

2.2.4 *Non-breeding behaviours*

Pied babblers roost communally in *Acacia erioloba* and *Acacia mellifera* trees, lining up along the high branches. After first light the group typically moves away from the roost tree and spends around 15 minutes allopreening and autopreening, before commencing foraging. Pied babblers are predominantly terrestrial foragers, spending >95% of their foraging time on the ground (Ridley & Raihani 2007a). Foraging typically takes two forms (A.R. Ridley unpublished data); the first is digging, where birds use their beak to dig in the sand for large invertebrates such as beetle larvae and small scorpions. The second is gleaning, where birds pick smaller items from the surface, such as termites and ants. Foraging takes place in a tight group, with individuals rarely more than 2 m apart, and the group flies between foraging patches. During the course of most days a pied babbler group will display at the borders of their territory, usually 1-3 km^2 in size. These displays can escalate into inter-group-interactions (IGIs), when the neighbouring group responds to the display. IGIs are stereotyped interactions that are played out as a call and response, they rarely escalate into physical fights (Golabek et al. 2012). Other interactions with non-group members occur when prospecting individuals are near to the foraging group, either cal

ling or directly interacting with the group, they are usually chased off by the group as a whole or by group members of the same sex as the prospecting individual (Raihani et al. 2010).

2.2.5 *Age*

Birds are termed as adults if they are >12 months old, or if they are an un-ringed immigrant into the population with adult plumage (pied; white and black/dark brown). Individuals are categorised as sub-adults when they are between 6-12 months of age, and any individual <6 months old is categorised as a juvenile (although referred to as a fledgling when dependent upon care-givers). Pied babblers show a very marked change in plumage during development; newly fledged individuals are a uniform brown, before slowly moulting their feathers, going through a mottled stage, and finally developing the adult plumage: all feathers white except the greater coverts, remiges (primaries and secondaries), alula and retrices, which all turn dark brown/black.

Age is always calculated as days post-hatching. Hatching date was determined by visiting the nest daily around the predicted hatching date. Fledging date was determined by visiting the group daily around the time offspring were predicted to fledge. Adults who immigrated into the population were assumed to be at least a year old, as the average age of dispersal is 565 days (Raihani et al. 2010), and their 'hatching date' is taken as a year prior to their immigration into the study population.

2.2.6 *Sexing*

Pied babblers are sexually monomorphic and therefore sexing was carried out using a PCR-based molecular sexing technique (Griffiths et al. 1998). When nestlings were ringed, at 11 days post hatching, and when immigrants into the population were ringed, a blood sample was taken by brachial venipuncture (ca 50 µl). The sample was stored in 700 µl of Longmire's Solution Blood Lysis Buffer, and kept at 4^{o}C. PCR was done with 50 ng DNA, buffer supplied by the manufacturer (Promega) diluted to 1X, 2.0 MgCl2, 10 picomoles of forward (P2: 5' - TCTGCATCGCTAAATCCTTT - 3') and reverse (P8: 5' - CTCCCAAGGATGAGRAAYTG - 3') primer, 4 picomoles of each dNTP, and 0.5 units of GoTaq DNA polymerase enzyme (Promega) in a 20

µL reaction. PCR cycle settings were: a denaturation step of 94°C for 2 minutes, amplification of 40 cycles of 94°C for 15 seconds, 50°C for 20 seconds, and 72°C for 25 seconds, then an extension step of 72°C for 1 minute. Birds were sexed according to the presence of the PCR products of CHD-Z (357 bases) and CHD-W (378 bases): males had one band while females had two bands. Differences between sexes could be seen through electrophoresis of PCR products in 3% agarose gel at 85V for three hours, or through electrophoresis in 4% acrylamide gel at 1200V for three hours (See Nelson-Flower (2009) for further details).

2.2.7 *Predators*

Terrestrial predators of pied babblers include yellow mongooses, slender mongooses, African wildcats (*Felis sivestris cafra*), small spotted genets (*Genetta genetta*), rock monitor (*Varanus albigularis*), cape cobras (*Naja nivea*) and puff adders (*Britis arietans*) (Ridley & Raihani 2007a). Aerial predators include pale-chanting goshawks (*Melierax canorus*), lanner falcons (*Falco biarmicus*), giant eagle owls (*Bubo lacteus*), pearl spotted owlets (*Glaucidium perlatum*), spotted eagle owls (*Bubo africanis*), martial eagles (*Polemaetis bellicosus*), black-breasted snake eagles (*Circaetus pectoralis*), black-shouldered kites (*Elanus axillaris*) and gabar goshawks (*Micronisus gabar*) (Ridley et al. 2013).

2.2.8 *Individual identification*

All individuals are individually ringed with a unique combination of three plastic colour rings and one metal ring. All individuals are ringed under the SAFRING licence number 1263. All nestlings are ringed 11 days after hatching. Adults birds that immigrate into the population are trapped using a walk-in trap; the bird is isolated from the rest of the group and then enticed into the trap using meal worms (*Tenebrio molitor* larvae). The metal rings all have a unique code, enabling identification if the bird loses all its colour rings. In the event of a bird losing all of its colour rings, it is trapped using the method outlined above but only if there are other birds in the group who also have lost all of their colour rings.

2.2.9 *Habituation*

All birds in the population are habituated to close human observation (less than 2 m). This proximity allows observers to record detailed behaviours without altering the babblers'

natural behaviour. It takes between six to 12 weeks to habituate a group of babblers to a level were an observer can walk with the group without causing any apparent distress or alarm to the birds (Ridley & Raihani 2007a). The groups are trained to associate a specific whistle with a food reward, meal worms, enabling us to find the birds quickly. The association of the whistle with a food reward is reinforced during the periods when we weigh the birds.

2.3 The Pied Babbler Project

The Pied Babbler Project was setup, in May 2003, and has been maintained by Dr Amanda Ridley. Since the establishment of the population Dr Nichola Raihani, Dr Martha Nelson-Flower, Dr Krystyna Jordan, Dr Matthew Bell, Dr Tom Flower and Dr Andy Radford have all conducted work on the population and contributed to the habituation of the study population. Since this time, daily weights and major life-history events have been recorded, leading to the collection of a vast database of non-invasive weights and life-history information.

2.4 Data collection

2.4.1 *Weights*

The babblers are trained to jump onto a top balance scale for a small food reward (<0.5g of boiled egg and two meal worms), the whistle is used to alert the birds to the fact that we want to carry out weights (Figure 2.4a & b). Weights are taken at the start and end of every session with the babblers, and are accurate to within 0.5 g. Morning weights are taken within 20 minutes of the group leaving the roost tree, evening weights are taken within 20 minutes of the group going to roost, and all other weights are considered as 'lunch weights'. Unless stated otherwise, morning weights were used for all analyses.

Figure 2.4a) weighing babblers. **b)** Babbler (MXYB) on the scale, weight 84.3g.

2.4.2 *Observational data collection*

Data in this thesis were collected over three field seasons: September 2009 – April 2010, October 2010- April 2011 and October 2011-March 2012. Two types of data were collected: behavioural data, collected either *ad libitum* or using time-activity focal observations (hereafter, 'focals'; Altmann 1974), and sound recordings. Data totalled over 295 hours of focal data on 104 fledglings from 17 different groups, over 337 hours of *ad libitum* behavioural observations and over 30 hours of sound recordings. During the collection of *ad libitum* data, the observer walked slowly with the group as they foraged and noted down the relevant behaviours. During *ad libitum* data collection (Martin & Bateson 2007), the following behaviours were recorded: all feeding events (including the identity of the feeder, the identity of the receiver and the item size); all sentinel behaviour (including sentinel identity); when a fledgling moved location (from ground to tree or from tree to ground); all instances of fledglings associating with adults ('social–foraging', including identities of adult and fledgling) (Thompson & Ridley 2013); all lead calling behaviour (Raihani & Ridley 2007a; Raihani & Ridley 2008a); and all instances IGIs. Focals involved the observer closely following a specific individual, usually for 20 minutes. The behaviours recorded during focal observations were: the duration of foraging bouts; type of foraging used (dig or glean); all prey items caught (size and type); location of fledgling (ground or tree); duration of all begging bouts (s); duration or all association interactions (s); identity of association partners; all prey items fed to fledgling; identity of all feeders; and identity of all sentinels. Focal observations were not carried out during IGIs or immediately after major predator alarms (when group members fled to the cover of trees and bushes; Ridley et al. 2013), as these may have affected normal foraging behaviour. If a focal had already started, it was

terminated upon the start of one of these events. Focal data collection was paused when the bird was out of sight and resumed when the bird was in clear view once more. If the break in observation was longer than 5 minutes, the focal observation was aborted.

Normally groups were found in the evening, either with them coming to the habituation whistle, being seen from a distance or being heard from a distance. The whistle usually causes the group to fly to the observer when the group is more than 200 m away or causes an individual to fly up to a vigilant perch, some groups even call to the whistle. Groups were followed to their roost tree and the location marked with a hand held GPS. The next morning the observer would return to the roost tree before first light to weigh the birds and then follow the group for 3-4 hours. Morning sessions make up the bulk of the observational and all of the experimental data, with some data coming from sessions in the evening.

All prey items caught or fed were categorized into different size classes. These size classes were then used to estimate the biomass either caught or consumed by offspring, using the same technique employed by Ridley & Raihani (2007b). The biomass for each size class was calculated from the average weight of 50 items for each class. Prey items were classified into five different size classes (Raihani & Ridley 2007a):

1. Tiny (0.01 g): bird was seen to eat food, but the item was too small to be seen.
2. Small (0.11 g): whole food item fits inside adult's bill.
3. Medium (0.45 g): up to half of food item protrudes from bill.
4. Large (0.84 g): half to ¾ of food item protrudes from bill.
5. Extra-large (1.5 g): most of item protrudes from bill.

Typically, there is a lag between rainfall and increased insect abundance (Cumming & Bernard 1997). Therefore, total rainfall in the previous two months (60 days) was included as a proxy for food availability in statistical models.

2.4.3 *Experimental data*

A variety of non-invasive experimental techniques were used in this research. These included playbacks of fledgling begging, conspecific and heterospecific alarm calls, as well as

supplementary feeding experiments. All playback sound files were created using Raven 1.4 © (Cornell Lab of Ornithology; Ithaca, NY, USA), and the amplitude of all files was normalized to a volume similar to the natural calls (as measured by a sound level meter, Voltcraft SL100 (Voltcraft™; Barking, UK)). All playbacks were created from calls collected from the pied babbler study population or from heterospecific species at the KRR, using the sound recording equipment listed below. Sound files were converted to .WAV files, uploaded onto an iPod (Apple Inc.™; Cupertino, CA, USA) and played through shoX mini speaker (Tevo™; South Africa). Playbacks were carried out to mimic the natural occurrence of the call. For example, when playing back begging calls, the speaker was placed at a height as close to that of a fledgling as possible and kept within 1 m of the experimental bird. Feeding experiments were used to change an individual's short-term energetic constraints. Feeding experiments involved supplementally feeding a specific individual with a varying number of meal worms (approximately 0.45g in weight). Feeding was carried out as quickly as possible and in a manner to minimize disturbance to the behaviour of non target group members.

Full details of all experimental protocols are given in the relevant chapters. This research was conducted under clearance from the Animal Ethics Committee, University of Cape Town; permit number R2012/2006/V15/AR.

2.5 Equipment

Both *ad libitum* and focal data were recorded on a handheld Palm T|X (2009 Palm Inc™; Sunnydale, CA, USA) on programmes I wrote using Pendragon Forms (2002-2007 Pendragon Software Corporation™; Buffalo Grove, IL, USA). All GPS locations were taken using a Garmin eTrex HC (Garmin International Inc™; Olathe, KS, USA). Whilst with the foraging group GPS points were taken every 15 minutes, as well as to mark the location of all IGIs, nests and roosts. All sound recordings were made using a RØDE NTG-2 condenser shotgun directional microphone, frequency response 20-20,000Hz ± 2 dB, with RØDE BLIMP windshield and shock mount system (2009 RØDE microphones™; Silverwater, NSW, Australia) and recorded onto a Microtrack II (2009 M-Audio™; IIrwindale, CA, USA) to be stored as a .WAV file. All sound analysis was carried out using Raven 1.4. All weights were collected using an Ohaus Scout Pro II SPU2001 (Ohaus Corp.™; Parisippany, NJ, USA) top balance scale.

2.6 Statistics

Statistical analysis was carried out using three statistical packages; R (version 2.15.0), Genstat 15th Edition (VSN International™; Rothamstead, UK) and SPSS version 21.0 (IBM Corporation™; Armonk, NY, USA). All tests were two tailed. Parametric statistics were used wherever possible, and if data did not meet the assumptions of parametric tests then it was either transformed or non-parametric tests were performed. Multivariate analyses were conducted using Linear Mixed Models (LMM) and Generalized Linear Mixed Models (GLMM).

Table 2.1 definitions of the terms used in model selection tables in this thesis

Symbol	Definition
AIC	Akaike's Information Criteria
AICc	Akaike's Information Criteria corrected for small sample size
Deviance	-2LogLikelihood
K	Number of parameters
P	P value
χ^2	Wald statistic
ΔAIC/ ΔAICc	Defference in AIC/AICc value for that model and the model with most support
ω_i	Akaike weight for the model *i*

2.6.1 *Model selection*

I used an information theoretic approach to investigate the factors that best predicted the response variables investigated. Due to the limitation in sample size that I had for the majority of my data, I used the Hurvich and Tsai correction for small sample sizes of Akaike's information criteria (AICc) (Hurvich & Tsai 1989; Burnham & Anderson 2002). AICc is used for small datasets, as using AIC as the basis for model selection when using small datasets can increase the probability of selecting models with too many parameters (overfitting) (Burnham & Anderson 2002).

$$AIC = 2k - 2\ln(L)$$

$$AICc = AIC + \frac{2k(k+1)}{n-k-1}$$

In the majority of models investigated in this thesis random terms were included to take into account repeated measures. I created a list of candidate models based on *a priori* hypotheses, each consisting of the basic model (with no predictor terms, only the constant, random terms and the residual variance) and a number of non-correlated explanatory terms. These alternate hypotheses were created by using my knowledge of the study system and the potential factors influencing the variable under investigation (Burnham et al. 2011). These *a priori* candidate models also contained interactions between the candidate explanatory terms. AICc values were generated for all *a priori* candidate models and subsequently all models were ranked in order of their AICc values. Models with lower AICc values were considered to have more explanatory power. The best models were deemed to be those with the lowest AICc value and the highest Akaike weight (ω_i); however, all models with a ΔAICc<5 were considered to have at least some support (Burnham et al. 2011). When more than one model was within 5 AICc units of the best model, the importance of explanatory terms was evaluated using predictor weights (Symonds & Moussalli 2011). Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable. Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011).

2.6.2 *pDFA*

Discriminant Function Analysis (DFA) is a classification technique, it generates linear combinations of variables (linear discriminant functions, LDs) that maximizes the probability of correctly assigning observations into pre-determined groups or new observations into these groups (Quinn & Keough 2002). Bioacoustics analysis has typically used DFAs to investigate differences in calls, for example given by individuals of different sexes. However, traditional DFAs only allow for the analysis of one factor, and so can only use one call per individual or bout, otherwise it violates the assumptions of the test (Mundry & Sommer 2007). Therefore, when using multiple calls from the same individual or investigating factors such as sex or social status, a DFA will be inadequate due to violating the assumptions of independence. In Chapter 3 I aimed to capture the structural changes in vocalizations that

occur within individuals over time, and the variation between sexes, broods and groups. Mundry & Sommer (2007), developed the Permuted Discriminant Function Analysis (pDFA): enabling classification with two-factorial data sets, and allowing subjects to be nested or cross with the grouping factor. Hence, I emploed pDFA in the bioacoustics analysis part of this thesis.

There are two requirements for DFA/pDFA analysis. Firstly, DFAs are very sensitive to outliers (Tabachnick & Fidell 2001), with data containing outliers being unlikely to reveal significance, even when a clear effect exists and the outlier lies in the effect. Hence, data containing outliers should be transformed using appropriate transformations before commencing analysis. Secondly, the number of parameters included must be smaller than the number of objects in the smallest class. For example, if there were eight subjects in one class and five in the other, then four predictor variables would be the maximum allowed. Otherwise, the level of discriminability will tend to be overestimated (Mundry & Sommer 2007).

The subset of data used in each DFA was balanced with regard to the number of replicates per subject, limited by the subject with the smallest number of samples. The number of predictor variables (parameters) used was then reduced so that it was smaller than the number of objects in the smallest class, as detailed above. Subsets of the data are selected at random to create 'original' balanced data sets. These datasets have equal numbers of replicates per subject. This process of creating balanced datasets was then repeated 100 times, in order to account for intra-subject variation. To determine the average number of correctly classified calls, DFAs were then performed on each of these 'original' datasets and cross-validated datasets, using the remaining unbalanced data. Next, randomized datasets were produced from the original data. Randomized data were produced by shuffling data either within or between subjects, keeping constant all effects other than the one being tested. From this randomized data, a series of balanced randomly selected datasets were created (1000 random data sets). DFAs were then run on these randomized datasets using the same methods as for analysis of the 'original' datasets. To determine the significance of original dataset, the number of randomized datasets (including the original dataset) that perform equal to or better than the original data set was divided by the total number of

datasets tested (including the original dataset). The null hypothesis in a pDFA is that the DFA is not better at classifying the original dataset than the randomized datasets.

Chapter 3

The structure of fledgling begging

The structure of fledgling begging

3.1 Abstract

Acoustic begging is a common feature of many mammalian and avian parent-offspring interactions. Begging has been seen as a physical manifestation of parent-offspring conflict and so has received considerable theoretical and empirical attention. However, investigation into the structure of offspring begging has mainly focused on altricial nestling birds, which are confined in a competitive environment. Using acoustic analysis and a series of experiments, I seek to understand the structure and function of fledgling begging calls in the cooperatively breeding pied babbler. I found no difference in the structure of fledgling begging calls at different ages or between the sexes. However, begging calls were individually distinct and contained information about fledgling hunger levels. Begging calls became more broadband and reduced in peak frequency with increased satiation levels. In addition, begging calls could be divided into two call types: *repeat* and *crescendo*. Repeat calls were given regularly while fledglings followed foraging adults, whereas crescendo calls were emitted just before feeding events. However, playback experiments found no difference in adult provisioning responses to these two different call types. Understanding how begging calls are used and the information they contain is key to understanding the function of offspring solicitation behaviours. These results corroborate previous work on mobile offspring, showing that multiple begging call types may be an adaptation to mobility.

3.2 Introduction

Solicitation behaviours are a common feature of parent-offspring interactions and occur in a variety of forms: from the gape colour of nestling birds (Kilner 1997; Saino et al. 2000) and the touching of parents' mouthparts by burying beetle (*Nicrophorus vespilloides*) larvae (Smiseth & Moore 2002), to the vigorous swimming of poison-arrow frog (*Dendrobates pumilio*) tadpoles (Weygoldt 1980). In mammals and birds, acoustic begging is one of the most striking forms of solicitation (Kilner & Davies 1999; Leonard & Horn 2001b; Bell 2007; Hudson & Trillmich 2007; Manser et al. 2008; Thorogood et al. 2011) and is seen as a physical manifestation of the conflict between offspring and parents over resource allocation (Trivers 1974; Godfray 1991). Most studies of the acoustic properties of offspring begging

have been carried out on nestling altricial birds (Leonard & Horn 2006), although there are notable exceptions (Manser & Avey 2000; Kunc et al. 2007). Nestling studies tend to follow a standard protocol: nestlings are taken from their nest, placed alone in a sound isolation chamber, fed until satiated, and periodically stimulated to beg (Jurisevic 1999; Kilner & Davies 1999; Madden et al. 2005; Leonard & Horn 2006; Anderson et al. 2010). These experiments provide information about how the acoustic parameters of nestling begging change in a controlled environment depending on a variety of factors (e.g. age, satiation and temperature; Leonard & Horn 2001; Leonard & Horn 2006; Anderson et al. 2010). However, ecological context is often lacking (e.g. the presence of siblings), and investigations into mobile offspring outside the nest are scarce (but see Redondo & Exposito 1990; Jurisevic 2003; Hauber & Ramsey 2003). This study investigates, in the wild, the acoustic properties of begging in fledgling pied babblers.

Cooperative breeding is characterised by extended periods of offspring care (Langen 2000; Clutton-Brock 2002). For cooperative birds, the post-fledging phase is very important for offspring development, because it often encompasses the longest period of parental care and includes the period of peak provisioning (McGowan & Woolfenden 1990; Langen & Vehrencamp 1999; Russell et al. 2004; Ridley & Raihani 2007a). Efficient communication during this period is therefore crucial to the growth and development of offspring. However, the post-fledging environment differs from that of the nestling environment: offspring are mobile, located away from the nest, less nutritionally dependent and can evade predators better than nestlings (Jurisevic 2003; Hauber & Ramsey 2003). Fledglings are also able to actively solicit care by following adult care-givers (Ridley & Huyvaert 2007; Thompson & Ridley 2013). In contrast, nestling birds are confined to a stationary environment where siblings are in close proximity when competing over food items during provisioning events (Kunc et al. 2007; Berg et al. 2013). Due to these differences, fledgling begging may have evolved different characteristics to nestling begging. Pied babbler fledglings accompany the foraging group and solicit care directly from foraging adults (Thompson & Ridley 2013). As such, their environment is more similar to that of the dependant phase of social mammals such as meerkats, banded mongooses (*Mungos mungo*) and dwarf mongooses (*Helogale parvula*), than to that of nestling birds. The fledgling environment for pied babblers is probably similar to that of other cooperatively breeding birds (McGowan & Woolfenden

1990; Heinsohn 1991), however fledglings remain relatively understudied in these species. Consequently, predictions about begging by pied babbler fledglings can be informed by work done on social mammals (Kunc et al. 2007; Bell 2008a; Manser et al. 2008; Madden et al. 2009b). The main prediction to be drawn from such research is that pied babbler fledglings are likely to have multiple types of begging calls, that are used in distinct contexts (Kunc et al. 2007).

Animals have been shown to produce calls that contain contextual information, from referential alarm calls (Seyfarth et al. 1980; Manser 2001) and information about predation risk (Bell et al. 2010; Townsend et al. 2011), to individual identity and kinship (Charrier et al. 2001; Sharp et al. 2005; Sharp & Hatchwell 2005; Townsend et al. 2012). The signals used in these communication systems often contain multiple components that convey information (Rowe 1999). The nestling begging signals of many species have been shown to have multiple elements (Kilner et al. 1999), from gape colour and posturing to wing flapping and acoustic begging (Kilner 1997; Saino et al. 2000; Jurisevic 2003). With many species producing multiple young, care-givers face a choice of who to provision at each feeding event. If the begging calls of all offspring were identical, then the efficiency of provisioning may be reduced, as randomly provisioning young has been shown to produce low quality offspring (Grodzinski & Lotem 2007). Thus, for care-givers to provision offspring in a way that could be optimal for both parties, they should asses who to feed. Begging signals containing information about offspring may make provisioning more efficient. Nestling begging calls have been found to encode information about offspring hunger, with hunger increasing chick begging rate in many species (Kilner & Davies 1999; Leonard & Horn 2001b; Butchart et al. 2003; Hauber & Ramsey 2003; Leonard & Horn 2006). Some studies have found an effect of hunger on the acoustic structure of begging calls (Sacchi et al. 2002; Leonard & Horn 2006; Anderson et al. 2010), whereas others have found no effect on acoustic features (Träger et al. 2006). Begging calls also have been shown to convey information about nestling age (Redondo & Exposito 1990; Jurisevic 1999; Hauber & Ramsey 2003; Anderson et al. 2010), sex (Saino et al. 2003), temperature (Leonard & Horn 2001b) and mass (Sacchi et al. 2002). Therefore, fledgling begging is also likely to contain information that care-givers may use in provisioning decisions.

In this chapter, I describe the structure and use of fledgling begging calls in the cooperatively breeding pied babbler. I asked (i) whether the proportion of time spent begging is influenced by fledgling age, by group composition, or by recent rainfall (which is a proxy for food availability) (ii) if there are distinct types of begging calls, and if so, the contexts within which they are used, and (iii) whether fledgling begging calls contain information about individual identity, sex, age, and hunger level.

3.3 Methods

3.3.1 *Study site and species*

I studied begging by 104 fledgling pied babblers, from 15 groups in the southern Kalahari Desert at the Kuruman River Reserve, South Africa between November 2009 and March 2012. During the study, group sizes ranged from 2-10 adults (individuals more than 12 months old, average group size 4.88 ± 0.25 S.E.) and 1-4 dependent fledglings (average 2.03 ± 0.11 S.E.). For a fuller description of pied babblers and the study population see Chapter 2.

In pied babblers, all adult group members contribute to the provisioning of nestlings and fledglings (Raihani & Ridley 2007a; Raihani & Ridley 2008a). Pied babbler fledglings remain dependent upon adult care-givers for food for up to nine weeks (Ridley & Raihani 2007a). During this period, fledglings actively follow and beg from foraging adults. Begging is both a vocal and visual display, with begging calls accompanied by wing fluttering and gaping. Fledglings appear to use two forms of begging calls: 'repeat' begs, used while moving with the foraging group; and 'crescendo' begs, used around feeding events (pers. obs.). Fledglings often follow care-givers between foraging areas, and are not restricted in their access to adults (with the exception of occasional aggression from care-givers (Raihani & Ridley 2008a)). I defined fledglings as young who had left the nest and who were still nutritionally dependent upon care-givers. Fledglings are considered to be nutritionally independent when they receive less than one feed per hour from adults (Ridley & Raihani 2007b). The age range for fledglings in this study was 14-96 days post-hatching.

3.3.2 *What factors affect proportion time spent begging?*

I investigated the factors which determined the proportion of time that fledglings invested in vocal begging. Detailed 20-minute time-activity focal observations (Altmann 1974) were

carried out on individuals between 20 and 130 days post-hatching. Fledglings were deemed to be begging when emitting acoustic begging calls and were deemed to have stopped when they had not vocalized for more than 5 s. I recorded the duration of begging bouts (s) and divided the total begging time by the focal duration to obtain the proportion of focal observation time that fledglings spent begging. This term was then set as the response term in a generalized linear mixed model (GLMM). Fledgling age (days post-hatching), number of adults and fledglings in the group, adult:fledgling ratio, fledgling sex and brood number (which brood of the season the individual was from) were all included as explanatory terms in the model. In addition, as a proxy for food availability (Cumming & Bernard 1997), total rainfall (mm) in the 60 days before the focal observation was carried out was included as an explanatory term. To determine if pre-hatching conditions had any effect on fledgling begging I also included the total rainfall in the 60 days before fledglings hatched (mm) as an explanatory term. All focals observations were entered onto a handheld PDA, Palm T|X handheld PDA (Palm Inc™).

3.3.3 *Do fledglings have distinct begging call types?*

Fledgling begging calls were recorded using a RØDE NTG-2 shotgun microphone (RØDE microphones™), onto a Microtrack II digital recorder (M-Audio™). All recordings were made within 1-3 m of the focal fledgling. Recordings were not made during inter-group-interactions or intragroup disturbances (eviction events, competitions for dominance or advertisement of breeding vacancies) and recordings were only made a minimum of 30 minutes after major predator alarms (where birds stopped foraging and moved to the cover of trees (Ridley et al. 2013)), as these may affect normal begging behaviour. If a recording had already started it was terminated upon the start of one of these events. All acoustic analysis and manipulation of sound files was carried out using Raven 1.4 (Cornell Lab of Ornithology). Only calls with excellent audio quality (low noise-to-call ratio and with no overlap with the calling of other individuals) were used in acoustic analysis.

To investigate if fledglings had distinct begging call types, I analysed single crescendo and repeat calls that were taken from the same sound file. To minimize any temporal or satiation effects, I used calls that were given adjacent in time. Calls were taken from 24 fledglings, each from a different brood to minimize any effect of brood similarity. One call of each type

was taken from fledglings at 30 and 50 days post-hatching, to enable me to determine if call types were consistently different through time. Parameters of call structure were measured (see below) and analysed using a discriminant function analysis (DFA; see Chapter 2).

To investigate the context in which different begging call types were used I measured how far each begging call was from the next feeding event (s) and the category of call (repeat or crescendo). This allowed me to determine if one call type had a closer association with feeding events than the other.

3.3.4 *How do adults respond to different begging call types?*

Having determined that fledgling begging calls could be split into two distinct types (see Results), I used experimental playbacks with a paired experimental design to determine if adults responded differently to crescendo and repeat begging calls. First, I conducted behavioural focal observations on individual fledglings for 20-minutes, recording all feeding events (including identity of feeder and prey item type and size). A second 20-minute focal observation was then conducted with the focal fledgling's begging supplemented by one of two playback treatments (details below). The second focal was started within two minutes of the end of the first focal. The focal with the playback was always conducted after the focal without the playback. This experimental designed was chosen because the playback was expected to elicit increased provisioning rates from care-givers, thus the first focal was a control to determine the baseline provisioning rate. If focals with playbacks had been carried out first then the provisioning rates in the second focal would not have been natural rates, due to the influence of satiation levels on fledging begging (Chapter 4). For each focal, prey item size and biomass were calculated using the methods detailed in Chapter 2, and the same method as Raihani & Ridley (2007). Provisioning rates were calculated as the total biomass provisioned to fledglings per minute of the focal (biomass.min^{-1}). I compared care-giver provisioning rates to the focal fledgling before and during the playback. Data collection was paused when the bird was out of view and resumed when the bird was once more in clear view. If the break in observation was longer than 5 minutes the focal observation was aborted.

Two treatments were conducted including the two different call types (see Results): 'repeat only' and 'crescendo and repeat'. 'Repeat only' playbacks looped eight different repeat begs, whereas 'crescendo and repeat' playbacks looped four different repeat begs and four different crescendo begs, alternating between crescendo and repeat. To control for treatment order the 'repeat only' and 'crescendo and repeat' playbacks were paired and conducted on consecutive days, with the order randomized in a balanced design. In order for playbacks to simulate natural begging, all calls were normalized to 68 dB (as measured by a sound level meter (Voltcraft SL100; Voltcraft)) and the begging rate was 24 begs.min^{-1} (which represents natural begging rate). To reduce the likelihood of an adverse group response to the playback, all playbacks were created from recordings of the experimental fledgling made in the preceding seven days, and playbacks were only carried out on groups with more than one fledgling. Playback files were uploaded onto an iPod (Apple Inc. ™) and playbacks were carried out using a shoX mini speaker (Tevo™). The speaker was attached to the observer's ankle, approximately 15 cm above the ground, and kept within 1.5 m of the experimental fledgling. Playbacks were conducted on 10 individuals from nine groups, controlling for fledgling age at 50 days post-hatching.

3.3.5 *Is begging call structure affected by age?*

To investigate whether the acoustic structure of fledgling begging calls changed with chick age I compared fledgling begging at two ages: 30 and 50 days post-hatching. These ages were chosen as they represented a period when fledglings started to spend a considerable period of time on the ground (30 days: Chapter 5) and when begging levels peaked (50 days). Multiple calls were analysed from individuals at these two ages, with a mean number of calls per individual of 8.46 ± 1.13 S.E. (range: 5-19) at 30 days and 8.46 ± 1.07 (range: 6-18) at 50 days. Calls were analysed using cross-classified permuted discriminant function analysis (pDFA: described below), as multiple calls from individuals were used from both 30 and 50 days. Due to using multiple calls from each individual at two ages I split up males and females and analysed them separately (Mundry & Sommer 2007). I analysed calls from six males from five groups, and seven females from six groups. For details on acoustic analysis of calls see below.

3.3.6 *Is begging call structure affected by sex?*

To determine whether males' and females' begging calls differed in their structure I compared the begging calls of male and female fledglings at 30 and 50 days post-hatching. By comparing begging calls between the sexes at two different ages I was able to determine if differences develop over the course of dependence. I used nested pDFAs to determine if begging calls of males and females were distinguishable, as individual identity is nested within sex. I analysed the calls of six males and seven females, with a mean of 9.83 ± 1.96 S.E. (range: 6-19) calls per male at 30 days, 7.83 ± 0.60 S.E. (range: 6-10) calls per male at 50 days, 7.29 ± 1.23 S.E. (range: 5-14) per female at 30 day, and 9.71 ± 1.93 S.E. (range: 6-18) calls per female at 50 days. For details on acoustic analysis of calls see below.

3.3.7 *Is begging call structure affected by hunger?*

To determine whether the structure of fledgling repeat begging calls was affected by fledgling hunger, I manipulated fledgling hunger levels using a supplemental feeding experiment. Sound recordings (sound focals) were made by following a single pied babbler fledgling at a distance of 1-3 m for a 20-minutes period and recording all of the begging calls they made. The fledgling was then fed five meal worms within a 5-minute period. Five meal worms weigh approximately 2.25g, amounting to approximately 1.4 times the biomass a fledgling would normally consume on average per 20-minutes (1.68 ± 0.059 g S.E., range 0–6.4 g), constituting a biomass likely to reduce a fledgling's short-term need. In addition, the provisioning of five meal worms reduces time spent begging but not to a level where begging is scarce (Chapter 4). A second 20-minute sound focal was then carried out. Feeding experiments were carried out at 40 days post-hatching. I chose 40 days as it represented a period of peak begging for fledgling (see Results). This experiment was carried out on seven individuals from six groups. Six repeat begging calls were extracted from the beginning, middle and end of each sound focal for acoustic analysis (Träger et al. 2006). A cross-classified pDFA was used to determine if fledgling begging calls before and after supplemental feeding were distinguishable. In addition to call structure I also analysed begging rate and time spent begging (in a method analogous to that used in focal observations). I calculated begging rate by summing the number of begging calls in the sound focals before and after the treatment, and converting these into a begging rate per

minute (beg.min^{-1}). For investigations of how call structure and begging rate change with satiation, only repeat begging calls were investigated, as these calls are given regularly while fledglings move throughout the group, hence any changes in these calls that reflect need may provide useful information to potential provisioners. In addition due to the association of crescendo begs with feeding events, they were not consistently dispersed throughout the sound file, making comparison difficult. To determine how hunger affected the use of crescendo calls, I calculated the rate of crescendo calls per feeding event and compared this rate between the sound focals conducted before and after supplemental feeding.

3.3.8 *Are begging calls individually distinct?*

To investigate whether fledgling begging calls were individually distinct, I asked whether fledglings' calls could be distinguished from those of their same-aged broodmates. I analysed the begging calls of 31 fledglings from 13 different broods from nine groups. Mean number of fledglings per brood was 2.46 ± 0.14 S.E. (range: 2-3), with a mean of 6.54 ± 0.24 S.E. begging calls analysed per fledgling. A nested pDFA was used for this analysis, as individual identity is nested within brood identity. For details on acoustic analysis of calls see below.

3.3.9 *Sound analysis*

Spectrograms were made with a Hann window, 512-point Fast Fourier Transform (FFT) sample size and 50% overlap. To avoid extraneous sound, only energies between 350 and 20,000 Hz were analysed. Various call characteristics were extracted from sonograms, to investigate different aspects of call structure. Call duration (s) was measure to determine the length of calls. To investigate the level of disorder within calls, aggregate and average entropy were measured, with higher values relating to greater disorder. Various frequency measures were extracted: centre frequency (Hz); 1st quartile frequency (Hz); 3rd quartile frequency (Hz); frequency 5% (Hz); frequency 95% (Hz); and mean peak frequency (Hz). To determine the importance of how broadband calls were, inter-quartile range bandwidth (Hz) and 90% bandwidth (Hz) were both measured. In order to measure call shape, measurements of the frequencies (Hz) at which maximum acoustic energy was present were made at 25%, 50% and 75% of the call using a spectral slice (amplitude plotted against frequency) (Townsend et al. 2011). To measure the shape of the start of the call (1st change (Hz)) I subtracted the frequency value at 25% of the call from the value at 50%. Similarly, to

measure the shape at the end of the call (2nd change (Hz)) I subtracted the frequency value at 50% of the call from the value at 75%. Therefore, a positive value for 1st or 2nd change indicates that the frequency at maximum acoustic energy is increasing, while a negative value indicates that it is decreasing.

3.3.10 *Statistical analysis*

Analyses were conducted using SPSS version 21.0 (IBM Corporation™) and R (v. 2.15.0). All non-normal data were appropriately transformed and all model residuals where checked for normality. To investigate what factors influenced the proportion of time fledglings spent begging, I created a set of GLMMs to investigate *a priori* hypotheses and a basic model that contained only the constant, random terms and residual variance. The effects of fixed terms were considered using maximum-likelihood estimation, and random terms (individual and group identity) were included to account for the potential influence of repeated measures. I used Akaike's Information Criterion (AIC) as the model selection criteria (Burnham & Anderson 2002; Burnham et al. 2011). Co-linearity was checked for all explanatory terms and correlated terms were never included in the same model. I then ranked the models in order of their AIC values: models with lower AIC values were considered to have more explanatory power. Overall the model with the highest Akaike weight (w_i) and lowest AIC value was considered the best model, but all models within ΔAICc <5 were considered to have at least some support (Burnham & Anderson 2002). When more than one model appeared to have some support (i.e. ΔAIC <5), the importance of explanatory terms was evaluated by calculating the predictor weight (Symonds & Moussalli 2011) for each term.

A DFA was used to investigate the distinguishability of different call types, followed by binomial tests to evaluate significance. However, regular DFAs do not allow for the analysis of two-factorial data sets without violating the assumptions of the test (Mundry & Sommer 2007). When regular DFAs were no longer appropriate I carried out pDFAs (Mundry & Sommer 2007). Prior to conducting DFAs and pDFAs, checks for collinearity were conducted and parameters with unacceptable variance inflation factors (VIFs) were excluded from analysis. Nested and cross-classified pDFAs were carried out to analyse if begging calls could be distinguished based on differences in sex, age, hunger and within brood identity. Nested pDFAs are used in analyses when the control factor is nested within the test factor, for

example individual identity is nested within individual age. Crossed pDFAs are used when each of the levels of the control factor exists in both levels of the test factors (R. Mundry pers. comm.). If call types were deemed to be distinguishable, linear mixed-effects models (LMMs) with individual identity fitted as a random term, were run on the acoustic parameters measured. To reduce the risk of inflated type I errors I used a Bonferroni correction to evaluate significance (Rice 1989). Multivariate analysis of variance (MANOVA) was used to investigate the factors important in determining the individuality of begging calls, due to the presence of multiple response variables (Quinn & Keough 2002).

3.4 Results

3.4.1 *What factors affect proportion of time spent begging?*

Throughout the period of nutritional dependence the mean proportion of time that fledglings spent begging ranged from 0.01 to 0.77 (mean: 0.24 ± 0.01 S.E.). The model containing the most support given the data contained the terms age, age^2, rainfall in the two months prior to the focal observation and adult number (Table 3.1, Chapter 3 Appendix Tables S1 & S2). Fledgling age followed a quadratic relationship with investment in begging, with begging initially increasing before peaking and then falling to a zero level of investment (Figure 3.1). Rainfall had a negative effect on begging investment; increased rainfall in the previous 60 days reduced the proportion of time fledglings spent begging. Adult number had a positive effect on begging investment.

3.4.2 *Do fledglings have distinct begging call types?*

Crescendo and repeat begging calls clearly separate along the LD1 axis (Figure 3.2). LD1 accounts for 92.46% of the variance, LD2 for 5.85% and LD3 for 1.69%. The relative contributions of the terms tested to each discriminant function are presented in table 3.2. Calls could be accurately separated into crescendo and repeat calls with 84.9% success. In contrast, correct classification of call types according to age was lower, calls could be classified into age (30 or 50 days) and call type (crescendo or repeat) with an accuracy of only 47.3%. Crescendo begs had a longer duration, lower average entropy and the frequency with maximum acoustic energy increased throughout the call, in contrast to repeat begs where it decreased in the second half of the call (Table 3.2). Figure 3.3 shows sonogram of a repeat and crescendo call.

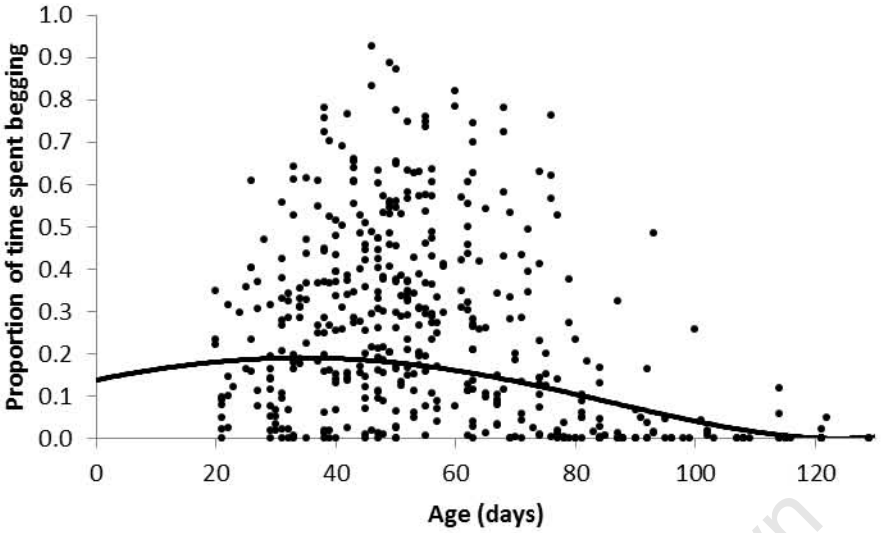

Figure 3.1 The relationship between age and proportion of time spent begging based on 489 20-minute focal observations of 104 fledglings in 15 pied babbler groups. The line shows the predictions from the best model investigating the factors affecting the proportion of time that fledgling spent begging (Table 3.1).

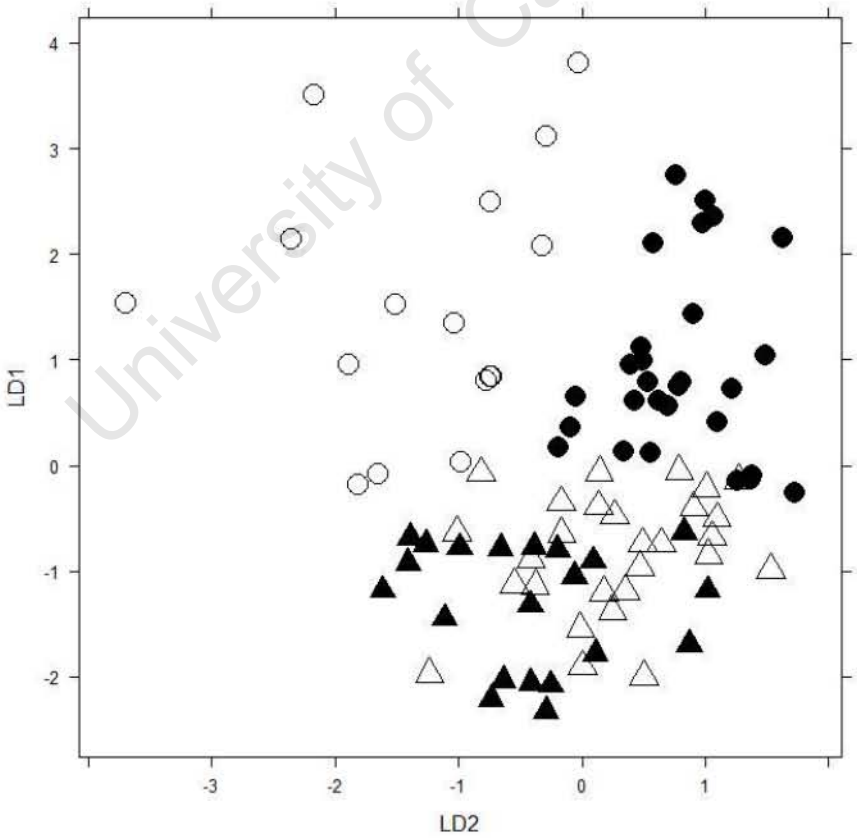

Figure 3.2 Plot of LD1 against LD2 from the DFA investigating repeat and crescendo begging calls. Triangles are repeat calls and circles are crescendo calls. Open shapes are 30 day old fledglings and closed are 50 day old fledglings.

Table 3.1 Model selection for the terms associated with the proportion of time spent begging by pied babbler fledglings. The response term was square-root of proportion of time spent begging. All GLMMs were fixed with individual and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. . Abbreviation: Fage= fledgling age; Fage^2= fledgling age squared; rnfl.b4.fcl= rainfall before focal observation (mm); Anum= number of adults in group; and brood= brood number for the season (1, 2 or 3). Only models with ΔAICc <5 are presented. N = 460.

Explanatory terms	Deviance	*K*	χ^2	AIC	ΔAIC	w_i		Effects ± S.E.
Fledgling age + Fledgling age² + Rainfall before the focal + Adult number	-101.1	8	195.65	-85.07	0	0.55	Fage:	0.004 ± 0.002
			23.49				Fage²:	$-5.44\times10^{-5} \pm 9.96\times10^{-6}$
			16.26				rnfl.b4.fcl:	$-4.68\times10^{-4} \pm 1.39\times10^{-4}$
			12.5				Anum:	0.026 ± 0.008
Fledgling age + Fledgling age² + Rainfall before the focal + Adult number + Fledgling number	-101.7	9	195.01	-83.7	1.37	0.28	Fage:	0.004 ± 0.002
			23.56				Fage²:	$-5.30\times10^{-5} \pm 1.01\times10^{-5}$
			16.18				rnfl.b4.fcl:	$-4.53\times10^{-4} \pm 1.40\times10^{-4}$
			12.3				Anum:	0.026 ± 0.008
			0.58				Fnum:	-0.009 ± 0.011
Fledgling age + Fledgling age² + Rainfall before the focal + Adult number + brood number	-102.2	10	194.86	-82.22	2.85	0.13	Fage:	0.004 ± 0.002
			23.59				Fage²:	$-5.51\times10^{-5} \pm 1.01\times10^{-5}$
			16.27				rnfl.b4.fcl:	$-5.15\times10^{-4} \pm 1.49\times10^{-4}$
			12.35				Anum:	0.024 ± 0.009
			1.14				brood: 1	0.000 ± 0.000
							brood: 2	0.026 ± 0.030
							brood: 3	-0.120 ± 0.218

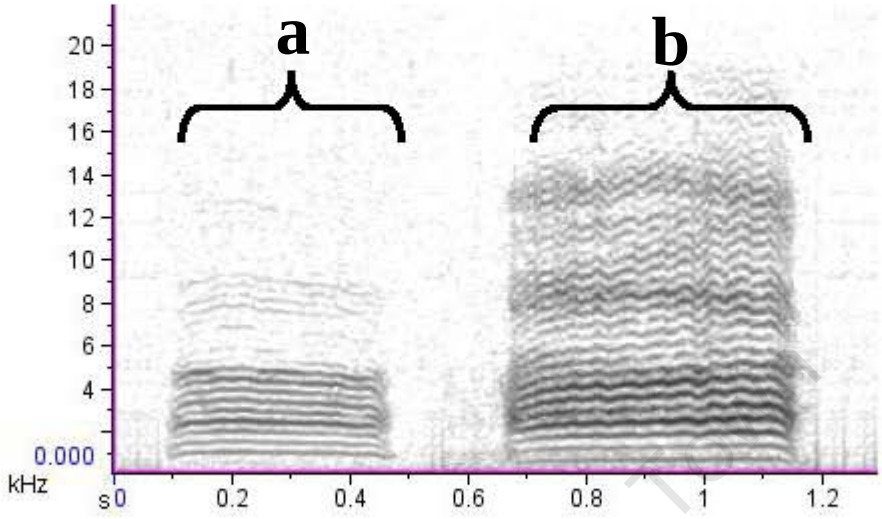

Figure 3.3 Spectrograms of pied babbler begging calls **a)** repeat beg **b)** crescendo beg. Hann window, 512 samples, 50% time overlap (Raven 1.4, Cornell Lab or Ornithology)

Table 3.2 Eigen values for the terms used in the DFA investigating crescendo and repeat begging calls.

	Eigen values		
Variable	**LD1**	**LD2**	**LD3**
Duration (s)	4.48	-1.78	4.54
Average entropy	-1.66	0.01	2.57
90% bandwidth	3.75×10^{-4}	-5.96×10^{-4}	-3.10×10^{-4}
Centre frequency (Hz)	2.00×10^{-3}	4.81×10^{-4}	3.50×10^{-4}
1st change (Hz)	-0.57	-0.88	0.53
2nd change (Hz)	0.04	-1.43	-1.7

Table 3.3 Mean values (± S.E.) of the variables important in the DFA investigating crescendo and repeat begging calls. Crescendo and repeat calls from 24 fledglings at 30 and 50 days post-hatching.

Variable	**Crescendo**	**Repeat**
Duration (s)	0.41 ± 0.02	0.30 ± 0.01
Average entropy	3.67 ± 0.05	3.82 ± 0.06
1st change (Hz)	50 ± 60	147 ± 56
2nd change (Hz)	78 ± 53	-93 ± 50

3.4.2.1 *Use of crescendo and repeat calls*

Crescendo begs were given much closer to feeding events than repeat begs. This was consistent at the ages of 30 and 50 days post-hatching. For 30 day old fledglings crescendo

begging calls were given at a mean of 2.78 s (± 0.44 s S.E.) before feeds compared to 19.72 s (± 0.64 s S.E.) for repeat begs (Mann-Whitney U test, U = 9792.0, $P < 0.001$: Figure 3.4). Similarly, crescendo begging calls were given at a mean of 4.51 s (± 0.76 s S.E.) before feeding evens compared to 22.82 ± 0.81 s for repeat begs when fledglings were 50 days post-hatching (Mann-Whitney U test, U = 15307.5, $P < 0.001$: Figure 3.4).

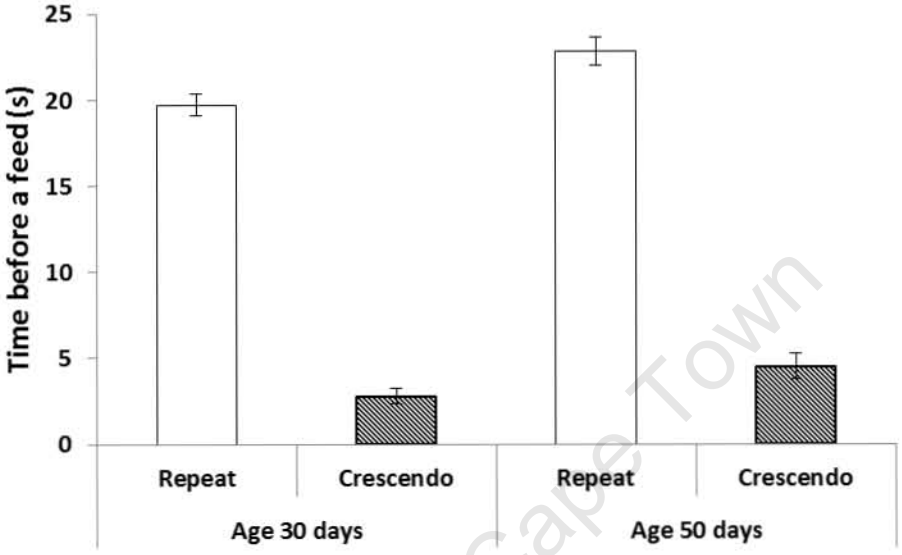

Figure 3.4 – Histogram showing the interaction between age and call type, and the duration of time before a feeding events that calls is given (mean ± S.E.).

Crescendo calls were given significantly sooner after the preceding begging call, at both ages 30 and 50 days, with a mean of 1.38 ± 0.13 s S.E. for crescendo and 2.78 ± 0.10 s S.E. for repeat at 30 days (Mann-Whitney U test, U = 39155.5, $P < 0.001$: Figure 3.5) and a mean of 1.31 ± 0.08 s S.E. for crescendo and 2.37 ± 0.04 s S.E. for repeat (Mann-Whitney U test, U = 39155.5, $P < 0.001$: Figure 3.5) at 50 days post-hatching.

3.4.3 *How do adults respond to different begging call types?*

There was no difference in the provisioning rate to fledglings before their begging was artificially increased (paired *t*-test, t = 0.31, *d.f.* = 8, $P = 0.762$), but adults significantly increased their provisioning rate when fledgling begging was artificially increased with repeat begs (from 0.07 ± 0.01 g.min^{-1} to 0.16 ± 0.02 g.min^{-1}; paired *t*-test, t = -4.25, *d.f.* = 8, $P = 0.003$) and with a combination of repeat and crescendo begs (from 0.06 ± 0.01 g.min^{-1} to 0.17 ± 0.01 g.min^{-1}; paired *t*-test, t = -6.21, *d.f.* = 8, $P < 0.001$; Figure 3.6). However, there was no significant difference in adult provisioning responses to playbacks containing

crescendo begs or to those with only repeat begs (paired *t*-test, t = -0.17, *d.f.* = 8, *P* = 0.869: Figure 3.6).

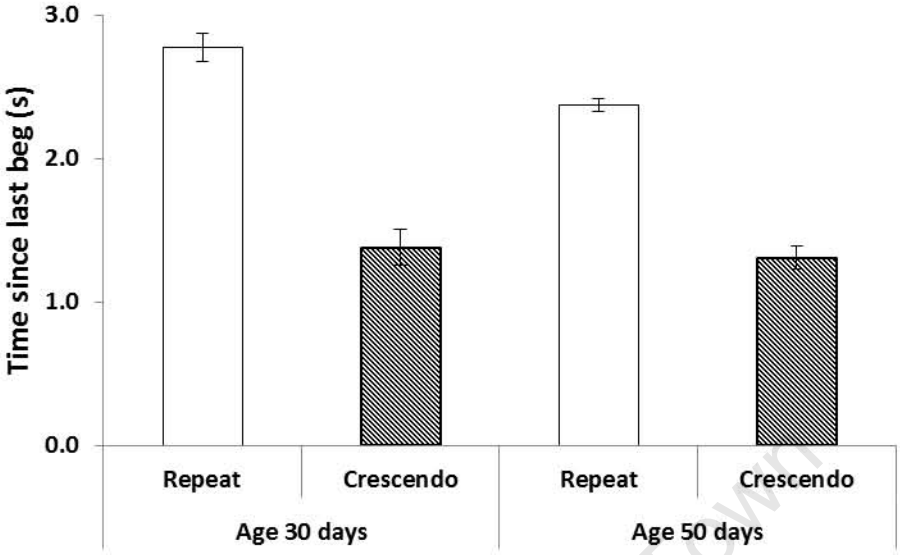

Figure 3.5. – Histogram showing the duration of time since the last beg that repeat and crescendo calls were given at 30 and 50 days of age (mean ± S.E.).

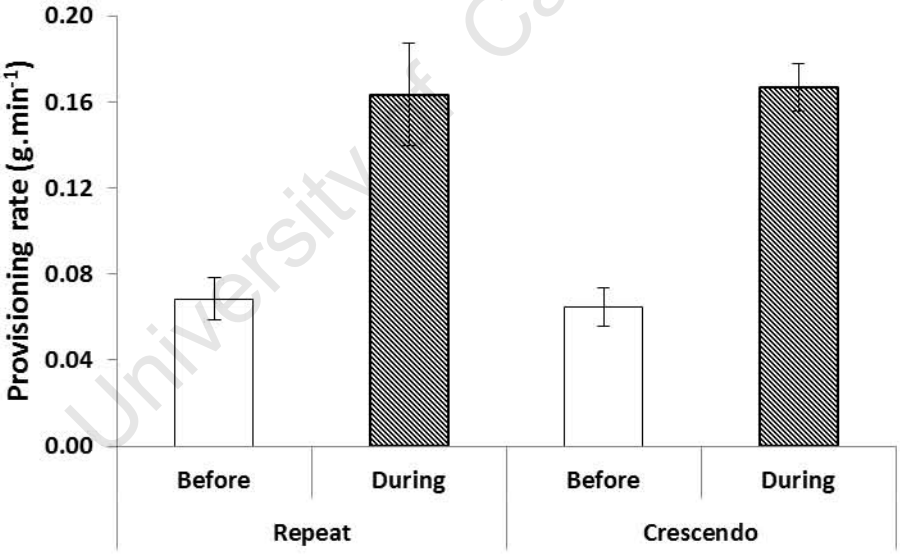

Figure 3.6. – Histogram showing provisioning rates to fledglings before and during experimental playbacks of 'repeat only' and 'crescendo and repeat' begging playbacks. (mean ± S.E.).

3.4.4 *Is begging call structure affected by age?*

There was no detectable difference in the acoustic structure of the begging calls of individuals at 30 days and 50 days post-hatching. Using a cross-classified pDFA it was not

possible to discriminate between males at 30 and 50 days post-hatching (number of correctly cross-classified elements = 17.87/1000, P = 0.823) nor between females at 30 and 50 days post-hatching (number of correctly cross-classified elements = 26.33/1000, P = 0.203).

3.4.5 *Is begging call structure affected by sex?*

There was no detectable difference in the acoustic structure of male and female fledgling begging. Using a nested pDFA it was not possible to discriminate between males and females at 30 days post-hatching (number of correctly cross-classified elements = 20.39/1000, P = 0.801) nor at 50 days post-hatching (number of correctly cross-classified elements = 18.37/1000, P = 0.649).

3.4.6 *Is begging call structure affected by hunger?*

Linear mixed-effects models (with individual fitted as a random factor) showed that 90% bandwidth (LMM Z = -3.493 P < 0.001) and peak frequency (LMM Z = 2.297 P = 0.022) varied significantly between begging calls at different satiation levels (Table 3.4). Fledgling begging became more broadband and decreased in peak frequency after supplemental feeding. A cross-classified pDFA showed that, overall, fledgling repeat begging calls could be correctly classified as either fed or not fed based on their acoustic structure (number of correctly cross-classified elements = 55.24/1000, P = 0.025).

There was a trend for a decrease in overall begging rate with increased satiation, with the mean begging rate before supplemental feeding being 11.6 ± 2.0 S.E. beg.min^{-1} and after 8.1 ± 1.4 S.E beg.min^{-1}. Although, this trend was not statistically significant (paired t-test, t = -2.06, $d.f.$ = 6, P = 0.085), fledglings did spend a significantly longer amount of time not begging after being supplementally fed (paired t-test, t = -4.52, $d.f.$ = 6, P = 0.004). Fledglings spent an average of 22.0 periods (± 2.6 periods S.E.) in silence after being supplementally fed, compared to 13.7 periods (± 2.1 periods S.E.) before. Supplemental feeding did not significantly affect the number of crescendo begs per feeding event. The mean number of crescendo begs per feeding event before supplemental feeding was 0.76 ± 0.23 S.E. and 0.98 ± 0.22 S.E. after (paired t-test, t = -1.13, $d.f.$ = 6, P = 0.302).

Table 3.4 Mean values (± S.E.), *Z* values and *P* values for each acoustic parameter analysed to investigate if hunger affects the acoustic structure of repeat begging calls. N=168

Acoustic parameter	Mean before ± S.E.	Mean after ± S.E.	*Z* value	*P* value
Duration (s)	0.302 ± 0.007	0.313 ± 0.013	-0.728	0.466
90% Bandwidth (Hz)	3892 ± 213	6115 ± 727	-3.493	**<0.001**
Interquartile bandwidth (Hz)	927 ± 52	1013 ± 99	-0.755	0.45
Peak frequency (Hz)	2343 ± 46	2129± 72	2.297	**0.022**
1st change (Hz)	51 ± 29	-31 ± 56	1.365	0.172
2nd change (Hz)	-99 ± 29	-1 ± 38	-1.761	0.078

3.4.7 *Are begging calls individually distinct?*

Using a repeated measures MANOVA, average entropy varied significantly between individuals within the same brood (Pillai = 0.054, $F = 6.52$, $P = 0.011$). A cross-classified pDFA showed that, within a brood fledgling repeat begging calls were individually distinguishable based on their acoustic structure (number of correctly cross-classified elements = 11.22/1000, $P = 0.010$).

3.5 Discussion

The results of this chapter show that fledgling investment in begging is highly variable, with a large range in the proportion of time that fledgling pied babblers spent begging. Pied babbler fledglings' begging investment varied with age. In addition, variation in proportion of time spent begging could be explained by environmental and social factors, such as rainfall in the preceding two months and number of adults in the group. In accordance with other studies of begging in mobile offspring, I found that pied babbler fledglings use two different begging call types and that these types were produced in distinct contexts. Furthermore, both hunger levels and individual identity were encoded in repeat begging calls. Therefore, fledgling begging has distinct call types that are used in specific contexts and contains additional information about fledgling identity and hunger that adults may be able to use.

Fledglings initially increase their begging after fledging, reaching a peak at around 40 days post-hatching, followed by a gradual decline and ceasing at around 120 days post-hatching. This decline in begging is mirrored by the increase in fledgling's foraging proficiency (Chapter 6) and is similar to results observed in spotted flycatchers (*Muscicapa striata*) (Davies 1976).

This result, suggests that fledglings may be reducing their investment in begging due to an increasing ability to meet their own nutritional demands. However, fledglings may also reduce their begging due to adults ceasing to respond to fledgling begging or because fledglings are unable to produce stimulating begging calls (reviewed in Madden et al. 2009a). The latter explanation seems less likely as I was unable to find any significant difference between fledgling begging at different ages. However, the period I investigated may have been too short and further investigation may reveal changes due to age over more extreme age gaps. I found a negative effect of rainfall in the preceding 60 days on the proportion of time that fledglings spent begging. As pied babblers predominantly feed on terrestrial invertebrates (Child et al. 2012) the negative effect of rainfall on fledgling begging levels is likely due to fledglings being fed at higher rates by care-givers and catching more prey from self-foraging due to high abundance in food (Cumming & Bernard 1997). Independent of the number of fledglings in the group, fledgling begging rate was higher in groups with larger numbers of adult care-givers. This might be a response to the adults' ability to provision fledglings (Grodzinski & Johnstone 2012), as the cost of providing care to fledglings is greater in smaller groups (Ridley & Raihani 2007a). Thus, adults in smaller groups may be less responsive to offspring begging and pied babbler fledglings may behave in a similar way to banded mongoose pups by reducing their begging investment towards unresponsive care-givers (Bell 2008a).

Similar to other mobile offspring, the begging calls emitted by pied babbler fledglings can be split into two types (Kunc et al. 2007): 'repeat' begs and 'crescendo' begs. Meerkat pups produce three types of begging call: high-pitched; repeat; and digging (Kunc et al. 2007). I did not investigate whether pied babbler fledglings used calls similar to the digging call of meerkat pups. The context in which pied babbler fledglings use their calls are similar to those of meerkats, with babbler crescendo begging calls being produced in urgent bouts prior to feeding events, similar to the high-pitched calls of meerkat pups (Manser & Avey 2000; Kunc et al. 2007). Being produced regularly outside of feeding events, the repeat calls of pied babbler fledglings and meerkat pups also appear to be analogous (Manser & Avey 2000; Kunc et al. 2007). Pied babbler fledglings inhabit an environment similar to that of meerkat pups, mobile and dispersed throughout the foraging group, thus the similarities in begging calls are not surprising (Manser & Avey 2000). Fledglings' use of begging calls is

different to that of nestlings, as with the exception of species that exhibit parent-absent begging (Roulin et al. 2000; Bulmer et al. 2008), most nestlings only beg when adults attend the nest (Leonard & Horn 2001a). The mobility of fledglings suggests that begging calls may be used to provide care-givers with constant information about offspring location and need, ensuring that an item found by an adult is fed to them and not eaten or fed to a sibling (Manser & Avey 2000). An additional, but not exclusive explanation, is that repeat calls could be used in sibling negotiation in a similar way to parent-absent begging (Roulin et al. 2000; Dreiss et al. 2010). By using repeat calls, fledglings could be communicating their intent to compete for the next feed to their siblings (Roulin et al. 2000). I was unable to test this hypothesis and it remains an area for future research. Combined with the meerkat results, this study suggests that multiple begging call types could be an adaptation to a mobile environment.

Despite the use of two call types by fledglings, my experimental results showed no significant difference in adult provisioning rates in response to playbacks of these two call types. Johnstone (2004) proposed that begging could serve two purposes: it could influence the level of provisioning or could influence the allocation of provisioning. The context in which these two call types were used, and their similarity to meerkat begging calls, suggest that repeat and crescendo calls could fit with these two purposes. Repeat calls may be used to influence adult provisioning rate, as adult provisioning rate in meerkats was influenced by the rate of repeat calls and not that of high-pitched calls (Manser et al. 2008). Kunc et al. (2007) showed that adult meerkats preferred to feed speakers broadcasting high-pitched begs (analogous to crescendo begs), suggesting that crescendo calls might determine allocation of food. However, the design of the experiment in my study was not a simple choice test between two different stimuli and may not have tested the difference in the call functions in the correct way. Nevertheless, my experiment does demonstrate that when crescendo begs are used outside of their normal context, just prior to feeding events, fledglings do not gain any additional provisioning benefit above the level achieved when only increasing repeat calls. If production costs (predation or energetic (Mock & Forbes 1992; Haskell 1994; Leech & Leonard 1996)) were the sole reason that crescendo calls were not used continuously, adult provisioning rates to the crescendo playbacks should have been higher. The fact that this was not the case goes against conventional wisdom in signalling

theory (Grafen 1990); it suggests that the crescendo calls are limited to specific contexts because use outside of these contexts may result in lower net benefits than just using repeat begging calls, rather than simply because of the costs of production. Although in this study I was unable to measure the costs of call production. There are two additional potential explanations for the lack of a difference in adult provisioning response between repeat and crescendo calls. Firstly, adults may associate crescendo calls with provisioning events and therefore if they hear them at a distance they may perceive that a provisioning event to that offspring has occurred and that they do not need to feed that fledgling or; secondly, adults may become desensitized to crescendo begs when exposed to high levels of them, although adults do not appear to become desensitized to repeat calls. Further experiments are needed to conclusively determine the function of crescendo and repeat begging calls and to measure the different costs associated with their production.

Multiple studies have shown that as offspring age the acoustic structure of their begging changes: increased duration of calls (Redondo & Exposito 1990; Jurisevic 1999), decreased duration of calls (Jurisevic 1999; Anderson et al. 2010) and increased frequency range (Anderson et al. 2010). These studies were all conducted on nestling birds, which are at a stage where development (growth in size) occurs faster than post-fledging (Gebhardt-Henrich & Richner 1998) and so their calls may be more likely to change with age. Due to physiological constraints, pied babbler fledglings may have reached a period of development where the structure of their calls no longer changes. However, other studies on offspring at similar life-history stages have shown acoustic changes in begging calls (Clemmons & Howitz 1990; Madden et al. 2009a). There is the potential for changes in pied babbler fledgling begging that are non-structural, akin to the increase in call rate in common cuckoos (*Cuculus canorus*) (Butchart et al. 2003). To a certain degree, this is shown in the result that fledgling age affects the proportion of time that fledglings spent begging. Alternatively, the age gap that I investigated (30-50 days) was too small to show an acoustic difference. Investigation of a greater age gap may show structural differences, and could shed light on the reasons for cessation of care (Madden et al. 2009a).

Unlike in other species (Redondo & Exposito 1990; Jurisevic 1999; Saino et al. 2003; Anderson et al. 2010), the begging calls of pied babbler fledglings were not distinguishable

between sexes. Sexually different begging calls are only likely to be beneficial in situations of sex-biased care. Monk et al. (1997) found no sex differences in the begging calls of western bluebirds (*Sialia mexicana*), attributing their results to a lack of sex-biased care in the species. Pied babblers are unlikely to show sex-biased care as neither sex is likely to have more reproductive value (Davies et al. 2012): the species is sexually monomorphic, both in terms of plumage and mass (Ridley & Raihani 2007a) and both sexes disperse and help raise young (Ridley & Raihani 2007a; Raihani et al. 2010; Nelson-Flower et al. 2012), although routes to dispersal do vary between the sexes (Raihani et al. 2010). Combined these two facts imply that it is unlikely that there is sex-biased preferential care, and so pied babblers are unlikely to benefit from being able to distinguish male and female offspring.

Honest signalling theory posits that offspring need varies in a cryptic way and that it has to be communicated to care-givers (Godfray 1991). The fact that the acoustic structure of fledgling begging changes depending on an individual's satiation level provides an additional signal which adults could use when making provisioning decisions, with multiple aspects of pied babbler fledgling solicitation potentially conveying hunger to care-givers (Rowe 1999; Chapters 4 & 5). Other species have also been shown to alter their begging calls depending on their hunger level (Leonard & Horn 2006; Manser et al. 2008; Anderson et al. 2010). Begging call structure containing information about offspring hunger adds to the results of Chapter 4, which show that adults reduce their provisioning to satiated fledglings. In addition, a change in begging call structure in relation to hunger is consistent with the idea that fledgling pied babbler begging is a reliable signal of hunger (Godfray 1991; Godfray 1995). However, additional experiments are needed to determine if adults use these acoustic differences to influence their provisioning behaviour.

The finding that begging calls are individually distinct is not novel or unexpected, as this has been shown in many other species (Monk et al. 1997; Brittan-Powell et al. 1997; Yasukawa et al. 2008). Physiological constraints, such as vocal tract length, could be the reason why begging calls were different between individuals (Fitch 1997). However, given the environment that fledgling pied babblers inhabit, individually distinct begging calls may be advantageous to both fledglings and care-givers (Tibbetts & Dale 2007). Unlike nestlings, fledglings tend to be dispersed (Manser & Avey 2000), repeatedly moving between adults

and are almost always within hearing range of all group members. Individually distinct begging calls may enable care-givers to locate and provision hungry individuals more effectively. Care-givers can respond appropriately to changes in individual begging levels and so optimize their provisioning. Again, this result fits very well with the results of Chapter 4, where I show that adult care-givers target their provisioning behaviour based on changes in individual fledgling begging levels. While it is possible that the ability to individually identify offspring may aid in the targeting of resources, it is equally likely that care-givers simply use offspring begging intensity to inform their provisioning decisions without keeping track of individual fledglings' begging effort.

These analyses have only dealt with the acoustic structure of fledgling begging and the proportion of time that fledglings invest in acoustic begging. Begging displays are not restricted to the auditory environment alone; many species use a variety of visual, physical and olfactory signals in their solicitation displays (Kilner 1997; Rauter & Moore 1999; Saino et al. 2000; Tanaka & Ueda 2005; den Boer & Duchateau 2006). In pied babblers, vocal begging is often accompanied by gaping and wing fluttering, similar to many other birds (Clemmons & Howitz 1990; Leonard & Horn 2001b) and therefore may be a multimodal signal (Kilner et al. 1999). It remains an area for future study to determine what factors (e.g. sex, age and hunger) affect these visual aspects of begging and how these signals are integrated with acoustic begging to influence provisioning rates.

Due to differences in their environment and development, fledglings and nestlings have different priorities that may shape their begging call structure (e.g. need to be located in the environment, are less dependent, more mobile and can evade predators: Jurisevic 2003). In this study, I show that fledgling pied babblers changed their investment in begging in relation to their age, and to environmental and social factors. Fledgling begging also encoded information about fledgling hunger and identity, which may be useful information for fledglings to signal and adults to receive. In addition, like other mobile offspring (Manser & Avey 2000; Kunc et al. 2007) pied babblers have distinct begging call types (repeat and crescendo), that are used in specific contexts. However, this study only investigated the begging of fledgling pied babblers. In order to determine if mobility has truly shaped begging

in this system, further investigation needs to be done to determine if nestling and fledgling begging systems are different in this species.

3.6 Chapter 3 Appendix

Full tables listing all candidate models tested

Deviance= -2log-likelihood output of each model; *K*= the number of parameters tested in each model; AICc= Akaike's information criterion for small data sets; ΔAICc= the models AICc minus the minimum AICc among candidate models. For each candidate model: Basic= basic model with no predictor terms, only the constant, the random terms and residual variance (σ^2); Fage = fledgling age (days); Fsex = fledgling sex (female or male); Anum = number of adults in the group; Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio; brood = brood number; rnfl.b4.hthc = cumulative rainfall for the two months preceding hatching; rnfl.b4.fcl = cumulative rainfall for two months prior to the focal. All GLMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. All models with ΔAICc <5 are in bold.

Table S3.1: Factors affecting proportion of time fledglings spent begging

Model	Deviance	*K*	AIC	ΔAIC
Fage+Fage²+rnfl.b4.fcl+Anum	-101.1	8	-85.07	0
Fage+Fage²+rnfl.b4.fcl+Anum+Fnum	-101.7	9	-83.7	1.37
Fage+Fage²+rnfl.b4.fcl+Anum+brood	-102.2	10	-82.22	2.85
Fage+Fage²+rnfl.b4.fcl+ADFL	-93.31	8	-77.31	7.76
Fage+Fage²+rnfl.b4.fcl+brood	-94.8	9	-76.8	8.27
Fage+Fage²+rnfl.b4.fcl	-90.44	6	-76.44	8.63
Fage+Fage²+Anum	-90.3	6	-76.03	9.04
Fage+Fage²+rnfl.b4.fcl+Fnum	-91.19	8	-75.19	9.88
Fage+Fage²+rnfl.b4.fcl+Anum+Fsex	-93.03	10	-75.03	10.04
Fage+Fage²+rnfl.b4.fcl+Fsex	-88.49	9	-72.49	12.58
Fage+Fage²+ADFL	-81.25	6	-67.25	17.82
Fage+Fage²	-80.27	7	-66.27	18.8
Fage+Fage²	-75.94	5	-63.94	21.13
Fage+Fage²+Fnum	-77.66	6	-63.66	21.41
Fage+Fage²+rnfl.b4.htch	-76.26	6	-62.26	22.81
Fage+Fage²+brood	-77.19	7	-61.19	23.88
Fage	-53.28	4	-43.28	41.79
rnfl.b4.fcl+brood	41.32	6	55.32	140.39
rnfl.b4.fcl+Anum	47.46	5	59.46	144.53
rnfl.b4.fcl+Fnum	47.56	5	59.56	144.63
rnfl.b4.fcl+ADFL	54.62	5	66.62	151.69
rnfl.b4.fcl	60.34	4	70.34	155.41
rnfl.b4.htch+Anum	61.69	5	73.69	158.76
rnfl.b4.fcl+Fsex	62.33	6	74.13	159.2

rnfl.b4.htch+Fnum	62.65	5	74.65	159.72
rnfl.b4.htch+Fsex	65.39	6	77.39	162.46
Anum	70.07	4	80.07	165.14
rnfl.b4.htch+ADFL	68.57	5	80.57	165.64
Fnum	75.74	4	85.74	170.81
rnfl.b4.htch	79.14	4	89.14	174.21
rnfl.b4.htch+brood	75.22	6	89.22	174.29
ADFL	82.61	4	92.61	177.68
brood	81.63	5	93.63	178.7
Fsex	84.89	5	94.89	179.96
basic	93.86	3	101.9	186.97

Table S3.2: Predictor weights for all variables investigating factors affecting fledgling begging

Predictor terms	Weight
Fledgling age (days)	**1.000**
Fledgling age²	**1.000**
Rainfall before focal	**0.994**
Adult number	**0.967**
Fledgling number	0.281
Brood number	0.141
Adult:fledgling ratio	0.011
Fledgling sex	0.005
Rainfall before hatching	6.12×10^{-6}

Predictor weights for the all variables investigated in GLMMs. Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable (Symonds & Moussalli 2011). Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011). All variables deemed to be important are in bold.

Chapter 4

The influence of siblings on pied babbler fledgling begging

Since the submission of this thesis for examination and prior to receiving the examiner's comments this work has been published as Thompson, A.M., Ridley, A.R., Hockey, P.A.R, Finch, F.M., Britton, A. & Raihani, N.J. (2013) *Animal Behaviour* 86, 811-819. A.R. Ridley, N.J. Raihani and P.A.R. Hockey assisted in discussion and commented on drafts of the manuscript. A. Britton and F.M. Finch assisted with data collection.

The influence of siblings on pied babbler fledgling begging

4.1 Abstract

Elaborate solicitation displays are a common feature of interactions between care-givers and offspring. These displays are interpreted as the phenotypic expression of the conflict of interests between parents and offspring over parental investment. Offspring typically do not exist in isolation, therefore they may adjust their begging in response to their siblings' begging, either competitively or cooperatively. Alternatively, begging may be independent of the begging efforts of siblings. Studies of avian begging have primarily focused on nestlings, where offspring are immobile and compete directly over the allocation of parental resources. I investigated the influence sibling begging had on individual fledgling begging in the cooperatively breeding pied babbler. Using experimental manipulations, I found that fledgling begging behaviour was negatively correlated with satiation and unrelated to the begging effort of siblings. Pied babbler care-givers were able to target increased provisioning to individuals with artificially increased demand while maintaining provisioning rates to the rest of the brood. Thus, fledglings were found to incur no provisioning costs or benefits from either increased or decreased begging by their siblings. I propose that the combination of targeted provisioning, flexible levels of provisioning and the dispersed nature of fledglings reduces the benefits of competitive or cooperative begging in this species.

4.2 Introduction

Complex and often elaborate communication systems that enable nutritionally dependent offspring to solicit food from care-givers have evolved in many taxa and in a variety of different circumstances (Cotton et al. 1996; Smiseth & Moore 2002; Smiseth & Moore 2007; Mas & Kölliker 2008; Bell 2008b; Mas et al. 2009; Madden et al. 2009a; Hinde et al. 2010). These displays are thought to be a physical expression of the underlying genetic conflict over the allocation of resources within families (Trivers 1974; Kilner & Johnstone 1997; Smiseth et al. 2008). Much recent work has focused on begging and solicitation as honest signals of individual need or quality (Kilner 1997; Godfray & Johnstone 2000; reviewed in

Mock et al. 2011). However, offspring typically do not exist in isolation and their begging behaviour may be influenced not only by their need or quality, but also by their siblings' begging behaviour (Bell 2007; Madden et al. 2009b; Marques et al. 2011; Romano et al. 2012). Investigating how offspring adjust their begging in relation to the begging behaviour of their siblings enables the understanding of whether begging functions to influence total levels of resources to the brood, or the allocation of provisioning within the brood (Johnstone 2004). In this study I investigated whether siblings influenced fledgling begging in the cooperatively breeding pied babbler.

Empirical studies to date have yielded mixed results in regards to how offspring respond to their siblings' begging (Johnstone 2004). In the simplest scenario, an individual's begging investment is solely determined by intrinsic factors; its condition, need or quality. If the begging of individual young is unaffected by the begging behaviour of its siblings, this would support the hypothesis that begging is a reliable signal of individual state or quality (Cotton et al. 1996; Kilner & Johnstone 1997). Some studies show that the begging effort of one offspring is not influenced by sibling begging effort (Kacelnik et al. 1995; Cotton et al. 1996). However, other studies have found that offspring alter their begging in response to their siblings' begging efforts (Smith & Montgomerie 1991; Price 1996; Leonard & Horn 1998; Roulin et al. 2000; Bell 2007). Broadly, if offspring adjust their begging effort in response to that of their siblings, they may do so either competitively or cooperatively. Competitive begging occurs when an individual escalates its own begging effort in response to increased begging from its siblings (Parker et al. 2002). Competitive begging is predicted to occur when offspring are competing over a fixed amount of resources (Godfray 1995; Royle et al. 2002; Johnstone 2004), with young increasing their begging intensity for a given level of hunger in attempts to outcompete their rivals (Trivers 1974; Briskie et al. 1994; Neuenschwander et al. 2003). Therefore, competitive begging influences resource allocation between individuals within a brood (Johnstone 2004) and has been documented in a number of studies (Smith & Montgomerie 1991; Price et al. 1996; Neuenschwander et al. 2003). Cooperative begging, on the other hand, occurs when begging influences the total amount of resources provisioned to the brood or litter (Johnstone 2004). When care-giver

provisioning is influenced by the collective begging intensity of the brood, offspring can gain direct benefits from the begging of their siblings (Bell 2007). Cooperative begging is expected to be most common where large competitive asymmetries exist between siblings and one offspring can dominate access to provisioning events (Johnstone 2004). Cooperative begging has also been documented in a number of studies (Mathevon & Charrier 2004; Kilner et al. 2004; Bell 2007; Madden et al. 2009b).

In this study, I experimentally manipulated pied babbler fledgling hunger levels and begging behaviour, respectively, to investigate how offspring responded to changes in their siblings' begging investment. Pied babblers provide an excellent model for the study of post-fledging begging because of their prolonged post-fledging dependent period, during which they use a mobile begging system to solicit care from adult care-givers (Ridley & Raihani 2007a; Thompson & Ridley 2013). The majority of empirical studies into begging behaviour have investigated the begging behaviour of nestlings (Hudson & Trillmich 2007; Kunc et al. 2007), who are confined in close proximity to their siblings, forcing them to compete directly over access to parental provisioning (Redondo & Castro 1992; Kilner 1995; Cotton et al. 1999; Manser & Avey 2000; Rodríguez-Gironés et al. 2001; Neuenschwander et al. 2003; Madden et al. 2009b). By studying mobile offspring it may be possible to gain a fuller understanding of the factors influencing offspring begging behaviour. The post-fledging period of development in cooperatively breeding birds offers an ideal situation in which to investigate mobile offspring, although it is relatively understudied because of the practical difficulties of following and observing fledglings (Langen 2000; Suedkamp Wells et al. 2007; Sankamethawee et al. 2009).

A series of experiments were used to determine: (i) how hunger affected fledgling begging; (ii) how fledgling begging affected adult provisioning rates; (iii) how fledgling begging behaviour was affected by the begging of their siblings; and (iv) how changes in adult provisioning behaviour to a target individual affected provisioning to siblings. For all three models of sibling response to competitors (non-responsive, competitive or cooperative begging) my predictions for the effects of hunger on begging and adult response are the

same: a positive relationship between hunger and begging investment and a positive relationship between begging effort and adult provisioning. However, predictions for sibling response and provisioning to siblings differ depending on which begging system is used. Under the competitive begging scenario, focal fledglings would be expected to increase their begging effort in response to a perceived increase in the begging effort of siblings. Furthermore, adults would be expected to increase provisioning to the chick that is begging the most, while decreasing provisioning to other fledglings in the brood. Under the cooperative begging scenario, focal fledglings are expected to decrease begging effort in response to a perceived increase in sibling begging. Adults would be expected to maintain or increase their provisioning levels across the brood if begging is cooperative.

4.3 Methods

4.3.1 *Study site and species*

Data were collected between November 2009 and March 2012 on fledglings from habituated pied babbler groups at the Kuruman River Reserve, in the southern Kalahari, South Africa. For further details about the ecology of pied babblers or the study population see Chapter 2. Pied babblers predominantly forage terrestrially (Ridley & Raihani 2007b), typically moving as a group between foraging patches. During the breeding season, when groups have dependent fledglings, pied babblers forage in fairly close groups that are typically spread out over a distance of 2-10 m (pers. obs.). Therefore, for the majority of the time all group members are within hearing range of fledgling begging during the post-fledging dependent period. Nutritionally dependent offspring move freely within the group, soliciting care from individual adults during short-term dyadic associations (Thompson & Ridley 2013).

4.3.2 *Behavioural observations*

Time-activity focal observations (hereafter, 'focals') (Altmann 1974) were recorded on dependent fledglings (29-80 days post-hatching). Focal observations were carried out on a single fledgling at a distance of 2-5 m. Focal observations were not carried out during inter-group-interactions or immediately after major predator alarms, and were terminated when

one of these events occurred. Data collection was paused when the bird was out of sight and resumed when the bird was again in clear view. If the break was longer than 5 minutes, the focal observation was aborted. If the bird was engaged in an activity (e.g. foraging) at the end of the 20 min focal observation, the observation was not terminated until it changed activity (Thornton 2008a). Due to these natural occurrences, focal length varied and averaged 19 min 38 s (± 6 s S.E.). Data collected included all items fed to fledglings by adults (prey type and estimated size (g)); time spent engaged in offspring-adult associations (s) (when fledgling was <50 cm from an adult, and was begging from and following that adult for >5 s); time spent begging (s) (when fledglings emitted begging calls); time spent foraging (s); and all items caught while foraging (prey type and estimated size (g)). All food item sizes and weights (g) were calculated using the methods described in Chapter 2 and used by Ridley & Raihani (2007a), and provisioning rates ($g.min^{-1}$) were calculated by dividing the total biomass fed (g) by the duration of the focal (min). A total of 506 behavioural focal observations were conducted on 103 fledglings from 15 groups (mean number of focal observations/fledging 5.80 ± 0.33 S.E., mean number of days between focals 10.01 ± 0.41 days S.E.). All observations were entered onto a handheld PDA, Palm T|X handheld PDA (Palm Inc™).

4.3.3 *Feeding experiment: how hunger affects begging*

I conducted feeding experiments to determine how changes in fledgling hunger levels affected their begging behaviour. Paired 20-minute focal observations (average duration: 19 min 31 s ± 8 s S.E.) were conducted on fledglings before and after supplemental feeding. Fledglings were fed a varying number of meal worms, in one of four treatments that simulated a range of satiation states: (i) 0 meal worms (0 g); (ii) 1 meal worm (~0.45 g); (iii) 5 meal worms (~2.25 g); and (iv) 10 meal worms (~4.5 g). Treatment (i) was a control, designed to have no experimental effect on hunger, whereas treatment (iv) was designed to have a large effect, representing ~2.5 times the biomass that a fledgling would normally consume in 20-minutes (A. Thompson, unpublished data). The proportion of focal time spent begging was used as the response term for analyses (detailed below). Both this and

the following experiment were carried out on 62 fledglings from 13 different groups, whose age ranged between 29-96 days post-hatching.

4.3.4 *Playback experiment: how begging affects provisioning*

I conducted playback experiments to determine how changes in fledgling begging affected care-giver provisioning behaviour. Paired 20-minute focals (average duration: 19 min 24 s ± 10 s S.E.) were conducted on fledglings before and during the treatment. Previous studies have used acoustic playbacks to artificially increase nestling begging (e.g. Muller & Smith 1978); I used a similar technique but with mobile fledglings. Each experimental fledgling's begging was artificially increased by using playbacks with a range of begging rates, to simulate different intensities of begging. The purpose of the first focal was to determine baseline provisioning rates to dependent fledglings. Playbacks were carried out during the second of the paired focals, using one of four treatments: (i) 0 begs.min^{-1}; (ii) 12 begs.min^{-1}; (iii) 24 begs.min^{-1}; and (iv) 36 begs.min^{-1}. Begging playbacks were created using calls from the focal chick recorded in the week prior to the experiment (previous studies have found that adults can discriminate offspring based on begging calls (Draganoiu et al. 2006)). All fledgling begging was recorded with a RØDE NTG-2 shotgun microphone (RØDE microphones™) onto a Microtrack II (M-Audio™). Playback calls were normalised at 68 dB, the natural amplitude of begging calls at 1 m from a begging fledgling (as measured by a sound level meter (Voltcraft SL100; Voltcraft)), using Raven Pro 1.4 (Cornell Lab of Ornithology). Playback files were uploaded onto an iPod (Apple Inc.™) and playbacks were carried out using a shoX mini speaker (Tevo™). To ensure that the begging playback was as natural as possible, speakers were placed at ankle height (~12 cm) and kept within 1 m of the experimental fledgling during the entire focal period, to ensure the begging calls were coming from as close to the experimental fledgling as possible, without disturbing the birds' behaviour. The distance between the speaker and non-experimental sibling varied between 1 and 10 m, as fledglings moved freely within the foraging group.

4.3.5 *Sibling begging response*

To determine whether fledgling begging behaviour was influenced by the begging of their siblings, control (parallel) focal observations were conducted *simultaneously* to experimental focals (as detailed above) on a randomly chosen sibling of the manipulated fledgling. Parallel focal observations were conducted by a second observer. Observers were randomly allocated to experimental or control fledglings and no difference due to observer was found in focal observation data. Parallel focal observations were carried out for both the feeding and the playback experiments. Identity of experimental and control fledgling was chosen randomly and using a balanced design. Because these parallel observations were done simultaneously with experimental observations they enabled the investigation of fledgling begging responses to sibling begging.

4.3.6 *Changes in provisioning to control siblings*

Parallel focal observations were also used to investigate if adult provisioning behaviour changed towards unmanipulated fledglings. Again, this was conducted for both the feeding and the playback experiments. This enabled me to determine if fledglings receive provisioning benefits or suffer provisioning costs due to changes in their siblings begging behaviour and subsequent changes in adult provisioning behaviour.

4.3.7 *Statistical analyses*

Experimental and control data were analysed separately to allow comparison between the behaviour of manipulated and control fledglings. I adopted an information-theoretic approach using Akaike's information criterion, with the Hurvich and Tsai correction for small sample size (AICc) (Hurvich & Tsai 1989; Burnham & Anderson 2002). Linear mixed models (LMMs) with normal distributions and identity link functions were used to determine the variables most important in influencing (i) the proportion of time spent begging by fledglings, and (ii) provisioning rates to fledglings ($g.min^{-1}$) by care-giving adults. The effects of fixed terms were considered using maximum-likelihood estimation. Group and individual identity were used as random terms to account for the effect of repeated measures on the distribution of the data. The other potential explanatory factors investigated in the models were fledgling age (days post-hatching), group size (number of adults), brood size (number

of fledglings), adult:fledgling ratio, focal type (before or after/during treatment), treatment (number of worms fed or playback rate (begs.min^{-1})) and interactions between these factors. I created a set of *a priori* candidate models, each with the basic model and a number of non-correlated explanatory terms. Using linear regression I checked for collinearity in all explanatory terms: correlated terms were never included in the same model. Models were then ranked in order of their AICc values, with models with lower AICc values being those with greatest explanatory power. Overall, the model with the highest Akaike weight (w_i) and lowest AICc value was considered the best , although all models with ΔAICc <5 were considered to have at least some support (Burnham & Anderson 2002). When more than one model appeared to have some support, the importance of explanatory terms was evaluated by calculating the predictor weight for each term using the method described in Symonds & Moussalli (2011).

Tests for normality were conducted on all data; if data were non-normally distributed they were transformed. Proportional data were arcsine-square-root transformed and non-proportional data were $\log_{10}$ or square-root transformed to achieve normality. When carrying out model selection, model residuals were checked for normality. All statistical analysis was performed using SPSS Statistics 21 (IBM corporation™).

4.4 Results

Babbler fledglings spent an average of 28.7% (± 1.76% S.E., range 0.0-76.4%) of focal observation time begging. Begging therefore represents a substantial proportion of a fledgling's time budget. During baseline focal observations fledglings were provisioned at a mean rate of 2.4 g.hour^{-1} (± 0.12 S.E., range 0-16 g.hour^{-1}), with a mean of 6.96 feeds.hour^{-1} (± 0.36 S.E., range 0-42 feeds.hour^{-1}).

4.4.1 ***Effect of hunger on begging***

Supplementally fed fledglings reduced their investment in begging as the number of meal worms they were fed increased (Tables 4.1; Figure 4.1). The effect of feeding on fledgling begging was significant even after the negative effect of fledgling age on begging investment

was controlled for. As fledglings became older they invested less time in begging (Table 4.1). For a list of all candidate models tested see Chapter 4 Appendix Table S4.1.

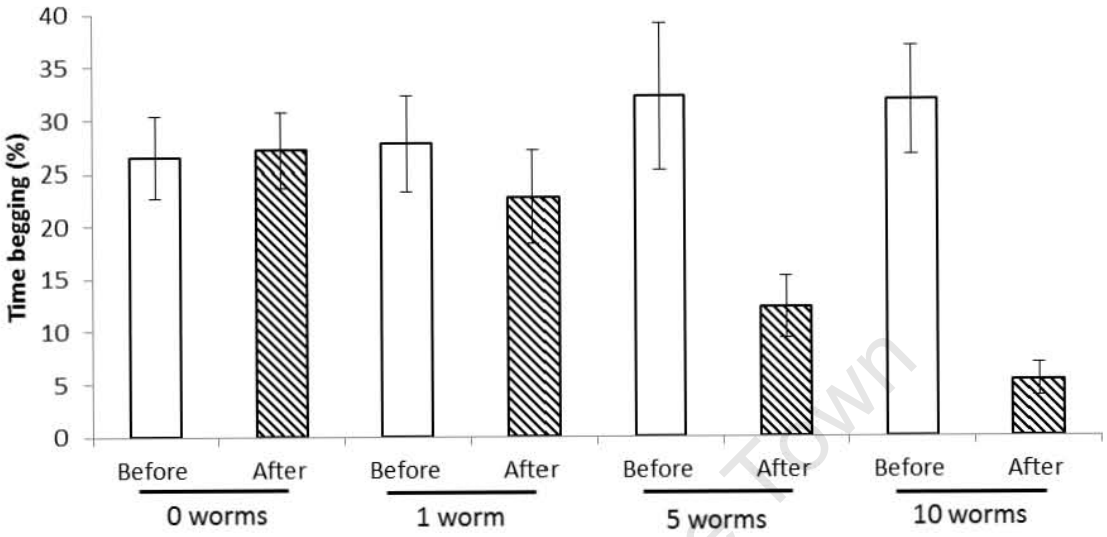

Figure 4.1 The effect of supplemental feeding on the percentage of time fledglings spent begging (mean ± S.E. of raw data); before and after fledglings were fed supplementary mealworms (number of supplemental worms: 1, 5 or 10). Paired comparisons were conducted on 58 individuals from 13 different groups.

4.4.2 *Effect of begging on provisioning*

Fledglings that had been fed more meal worms, and hence begged less, were provisioned at lower rates during the post-feeding focals than the pre-feeding focals (Table 4.2; Figure 4.2a). All candidate models tested are listed in Chapter 4 Appendix Table S4.2. Fledglings whose begging levels had been artificially increased through begging playbacks were provisioned at higher levels during playback-focal observations than during the pre-playback focal observations, with provisioning rate increasing with playback begging rate (Table 4.3; Figure 4.2b). For a list of all candidate models tested see Chapter 4 Appendix Table S4.3.

Table 4.1 Model selection for the terms associated with the proportion of time that experimental fledglings spent begging in the feeding experiment. Analysis was conducted on 58 fledglings from 13 groups. All LMMs included individual and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. Abbreviations: 0, 1, 5 & 10 represent the number of worms fed; Fage = fledgling age (days post-hatching); Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio in the group. Only models with ΔAICc <2 are shown in the table. N = 96.

Model	Deviance	*K*	AICc	ΔAICc	w_i	Effect ± S.E.	
Focal*worm number + Fledgling age (days)	570.02	10	593.96	0.00	0.17	before*0	3.210 ± 0.555
						before*1	3.408 ± 0.546
						before*5	4.262 ± 0.526
						before*10	4.615 ± 0.432
						after*0	3.337 ± 0.555
						after*1	3.296 ± 0.546
						after*5	1.884 ± 0.526
						after*10	0.000 ± 0.000
						Fage	-0.019 ± 0.012
Focal*worm number	572.45	9	594.05	0.10	0.16	before*0	3.110 ± 0.552
						before*1	3.366 ± 0.548
						before*5	4.279 ± 0.529
						before*10	4.615 ± 0.440
						after*0	3.238 ± 0.552
						after*1	3.254 ± 0.548
						after*5	1.901 ± 0.529
						after*10	0.000 ± 0.000
Focal*worm + Fledgling age (days) + Fledgling number	569.08	11	595.39	1.43	0.08	before*0	3.161 ± 0.555
						before*1	3.318 ± 0.549
						before*5	4.177 ± 0.530
						before*10	4.615 ± 0.433
						after*0	3.288 ± 0.555
						after*1	3.206 ± 0.549
						after*5	1.800 ± 0.530
						after*10	0.000 ± 0.000
						Fage	-0.019 ± 0.012

						Fnum	0.206 ± 0.210
Focal*worm number + Fledgling age (days)+ Adult:fledgling ratio	596.15	11	595.46	1.51	0.08	before*0	3.249 ± 0.553
						before*1	3.368 ± 0.544
						before*5	4.233 ± 0.524
						before*10	4.615 ± 0.434
						after*0	3.376 ± 0.553
						after*1	3.256 ± 0.544
						after*5	1.856 ± 0.524
						after*10	0.000 ± 0.000
						Fage	-0.019 ± 0.012
						ADFL	-0.114 ± 0.120
Focal*worm number + Fledgling number	571.54	10	595.48	1.52	0.08	before*0	3.060 ± 0.553
						before*1	3.278 ± 0.552
						before*5	4.196 ± 0.532
						before*10	4.615 ± 0.441
						after*0	3.188 ± 0.553
						after*1	3.166 ± 0.552
						after*5	1.818 ± 0.532
						after*10	0.000 ± 0.000
						Fnum	0.200 ± 0.208
Focal*worm number + Adult:fledgling ratio	571.57	10	595.51	1.55	0.08	before*0	3.148 ± 0.550
						before*1	3.326 ± 0.547
						before*5	4.249 ± 0.527
						before*10	4.615 ± 0.441
						after*0	3.275 ± 0.550
						after*1	3.214 ± 0.547
						after*5	1.871 ± 0.527
						after*10	0.000 ± 0.000
						ADFL	-0.113 ± 0.119

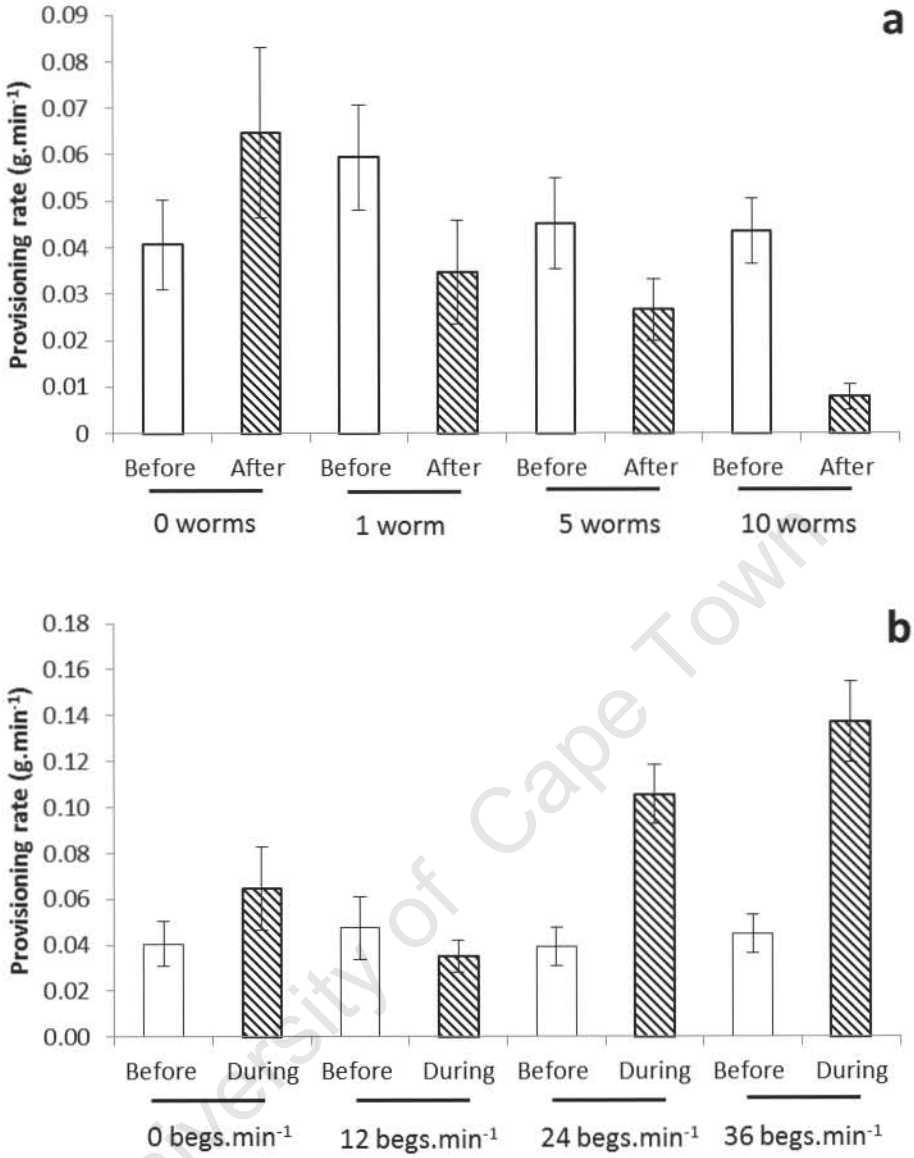

Figure 4.2a) The effect of supplemental feeding on the provisioning rate to fledglings (mean ± S.E. of raw data); before and after fledglings were fed supplementary mealworms (number of supplemental worms: 1, 5 or 10). Paired comparisons were conducted on 58 individuals from 13 different groups. **b)** The effect of artificial begging playbacks on the provisioning rate to fledglings (mean ± S.E. of raw data); before and during playbacks of fledgling begging (begging playback rates: 12, 24 or 36 begs.min^{-1}). Paired comparisons were conducted on 48 individuals from 13 different groups.

4.4.3 *Effect of siblings on begging*

During the feeding experiment, the begging behaviour of control fledglings was not influenced by any of the treatments on the experimental fledglings (Chapter 4 Appendix Table S4.4; Figure 4.3a). Similarly, during the playback experiment, begging behaviour of control fledglings was also not influenced by the artificially elevated begging of the

experimental fledglings (Chapter 4 Appendix Table S4.5; Figure 4.3b). The highest predictor weight was for adult number (0.30), but the basic model was the best model and therefore I conclude that none of the variables measured strongly predicted the begging behaviour of control fledglings. In addition, the begging behaviour of experimental fledglings was not influenced by the experimental playbacks (Chapter 4 Appendix Table S4.6).

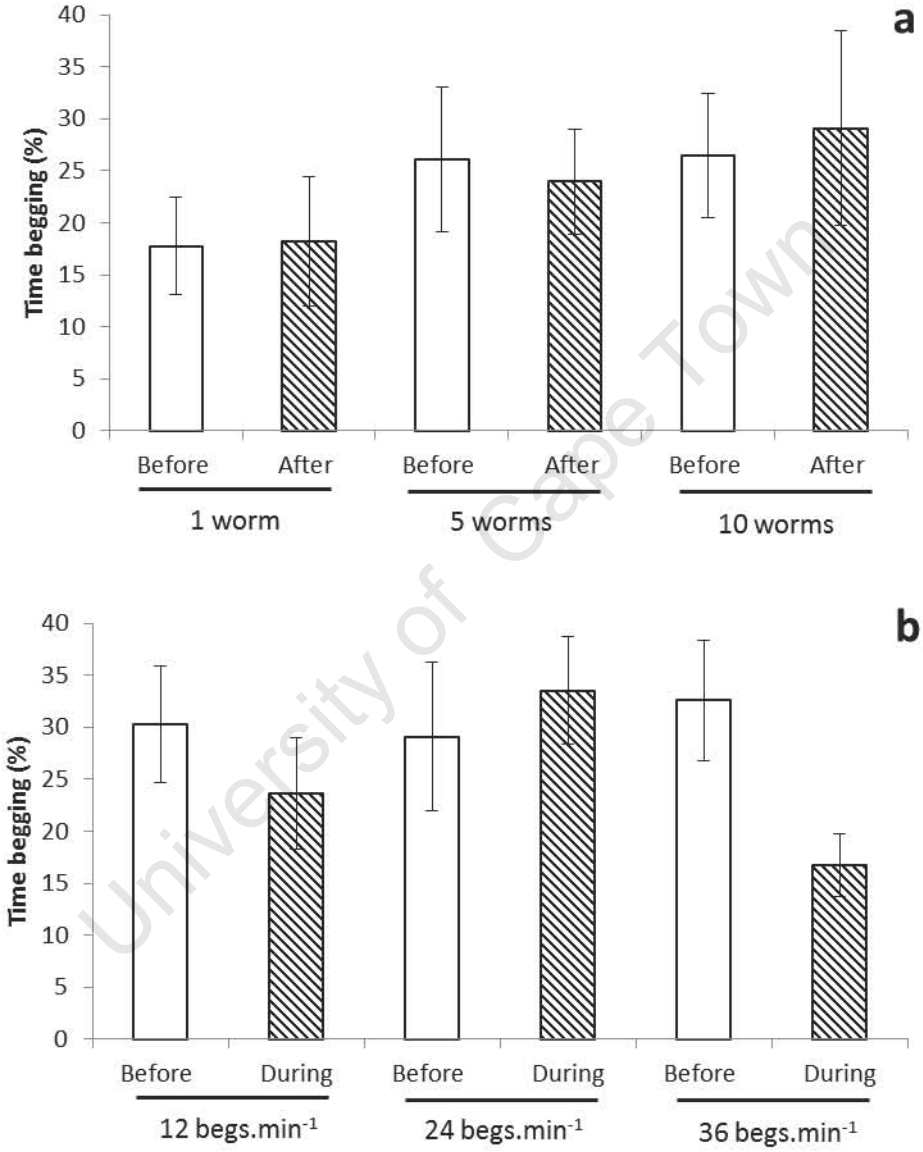

Figure 4.3a The effect of decreasing sibling begging, by supplemental feeding, on the percentage of time spent begging by fledglings (mean ± S.E. of raw data); before and after their siblings were fed supplementary mealworms (number of supplemental worms: 1, 5 or 10). Paired comparisons were conducted on 31 individuals from 12 different groups. **b** The effect of artificially increasing sibling begging on the percentage of time fledglings spent begging (mean ± S.E. of raw data); before and during playbacks of fledgling begging to their siblings (begging playback rates: 12, 24 or 36 begs.min^{-1}). Paired comparisons were conducted on 26 individuals from 11 different groups.

Table 4.2 Model selection for the terms associated with the provisioning rate (g.min^{-1}) to experimental fledglings in the feeding experiment. All LMMs included individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. The same abbreviations as listed in Table 4.1. Only models with ΔAICc <2 are shown in the table. N = 116.

Model	Deviance	*K*	AICc	Δ AICc	w_i	Effect ± standard error	
Focal*worm number + Fledgling age (days)	-241.96	10	-218.02	0.00	0.36	before*0	0.120 ± 0.035
						before*1	0.145 ± 0.035
						before*5	0.138 ± 0.034
						before*10	0.170 ± 0.029
						after*0	0.159 ± 0.035
						after*1	0.097 ± 0.035
						after*5	0.083 ± 0.034
						after*10	0.000 ± 0.000
						Fage	-0.003 ± 0.001
Focal*worm number + Fledgling age (days) + Adult:fledgling ratio	-242.81	11	-216.50	1.52	0.17	before*0	0.122 ± 0.035
						before*1	0.143 ± 0.035
						before*5	0.136 ± 0.033
						before*10	0.170 ± 0.029
						after*0	0.160 ± 0.035
						after*1	0.095 ± 0.035
						after*5	0.081 ± 0.033
						after*10	0.000 ± 0.000
						Fage	-0.003 ± 0.001
						ADFL	-0.007 ± 0.007
Focal*worm number + Fledgling age (days) + Fledgling number	-242.34	11	-216.03	1.99	0.13	before*0	0.118 ± 0.035
						before*1	0.142 ± 0.035
						before*5	0.135 ± 0.034
						before*10	0.170 ± 0.029
						after*0	0.157 ± 0.035
						after*1	0.094 ± 0.035
						after*5	0.079 ± 0.034
						after*10	0.000 ± 0.000
						Fage	-0.003 ± 0.001
						Fnum	0.008 ± 0.013

Table 4.3 Model selection for the terms associated with the provisioning rate (g.min^{-1}) to experimental fledglings in the playback experiment. All LMMs included individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. Abbreviations: 0, 12, 24 & 36 represent the begging rate of the playback (begs.min^{-1}); Fem = female; Mal = Male. Only models with ΔAICc <2 are shown in the table. N = 96.

Model	Deviance	*K*	AICc	Δ AICc	w_i	Effect ± S.E.	
Focal*Playback rate + Fledgling age (days)	-209.25	10	-185.22	0.00	0.33	B4*0	-0.195 ± 0.043
						B4*12	-0.189 ± 0.045
						B4*24	-0.200 ± 0.039
						B4*36	-0.163 ± 0.045
						DUR*0	-0.156 ± 0.043
						DUR*12	-0.192 ± 0.045
						DUR*24	-0.055 ± 0.039
						DUR*36	0.000 ± 0.000
						Fage	-0.003 ± 0.001
Focal*Playback rate + Fledgling age (days) + Adult:fledgling ratio	-210.66	11	-184.24	0.99	0.20	B4*0	-0.189 ± 0.043
						B4*12	-0.182 ± 0.045
						B4*24	-0.203 ± 0.039
						B4*36	-0.163 ± 0.044
						DUR*0	-0.151 ± 0.043
						DUR*12	-0.185 ± 0.045
						DUR*24	-0.057 ± 0.038
						DUR*36	0.000 ± 0.000
						Fage	-0.003 ± 0.001
						ADFL	-0.009 ± 0.007
Focal*Playback rate + Fledgling age (days)*Fledgling sex	-209.82	15	-183.40	1.82	0.13	B4*0	-0.187 ± 0.044
						B4*12	-0.185 ± 0.056
						B4*24	-0.196 ± 0.039
						B4*36	-0.163 ± 0.045
						DUR*0	-0.149 ± 0.044
						DUR*12	-0.188 ± 0.046
						DUR*24	-0.051 ± 0.039
						DUR*36	0.000 ± 0.000
						Fem*Fage	-0.003 ± 0.009
						Mal*Fage	-0.003 ± 0.008

4.4.4 *The effects of changing adult provisioning behaviour on siblings*

When provisioning rate to experimentally supplemented fledglings decreased there was no significant effect on provisioning rate to control siblings (Chapter 4 Appendix Table S4.7). Based on the predicted weights, the most significant factor affecting provisioning rate to control fledglings was age, with provisioning decreasing with increased age (Chapter 4 Appendix Table S4.9).

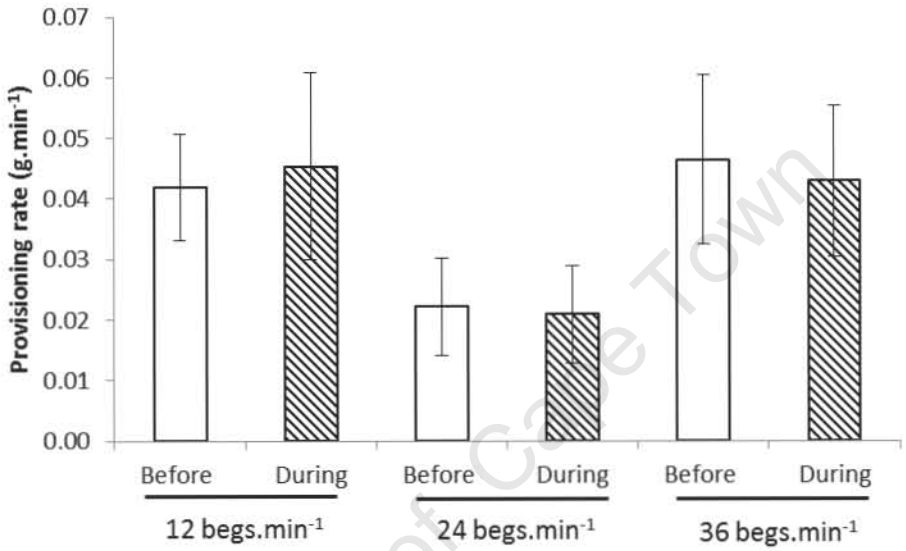

Figure 4.4 The effect of artificial begging playbacks on the provisioning rate to control siblings (mean ± S.E. of raw data); before and during playbacks to experimental fledglings (begging playback rates: 12, 24 or 36 begs.min^{-1}). Paired comparisons were conducted on 26 individuals from 11 different groups.

Experimental playbacks increased the provisioning rate to target fledglings. However, these playbacks produced no significant effect on provisioning to the control siblings (Chapter 4 Appendix Table S4.8; Figure 4.4). Based on the predicted weights, the most significant factor affecting provisioning rate to control fledglings was age, with provisioning decreasing with increased age (Chapter 4 Appendix Table S9).

4.5 Discussion

The main results of this chapter were that fledgling begging behaviour was positively correlated to fledgling hunger, in line with studies of nestling begging (reviewed in Mock et al. 2011). In addition, care-givers' provisioning levels were positively correlated with offspring begging behaviour. Fledglings did not change their begging investment in response

to changes in their sibling's begging behaviour. Lastly, fledglings suffered no provisioning costs nor gained any provisioning benefit from changes in their sibling's begging behaviour. Therefore, pied babbler fledgling begging is neither competitive nor cooperative, with these results showing that individual begging is apparently unrelated to sibling begging. Consequently, the begging of fledgling pied babblers seems to be a reliable signal of offspring hunger (Godfray 1991; Godfray 1995; Johnstone & Kilner 2011).

The begging behaviour of fledgling pied babblers is positively related to hunger levels, with more satiated individuals investing less time in begging. Care-giver response to begging also follows a positive relationship, with provisioning rates increasing with higher levels of begging. These two results are consistent with fledgling pied babbler begging being a signal of hunger (Mock et al. 2011). Many studies have shown these results in a variety of species (reviewed by Mock et al. 2011). However, to my knowledge this is the first experimental investigation into fledgling begging. Given that provisioning increases to match demand, why should fledglings reduce their begging when satiated? The benefit of extra provisioning gained from further begging is outweighed by the cost of continued begging. There are four possible potential costs that fledglings may incur. Firstly, begging may impose some form of predation cost (Haskell 1994) and so only fledglings who stand to gain fitness benefits, those most in need, should invest in begging (Godfray 1991). However, the costs of fledgling begging in this species have yet to be quantified and so this theory remains untested. Secondly, individuals within a group are highly related, as the dominant pair produce more than 95% of the offspring (Nelson-Flower et al. 2011), kin selection may therefore favour offspring to beg only in relation to their hunger, reducing the costs incurred by their broodmates and care-givers (Johnstone & Grafen 1992). Thirdly, during the fledgling period offspring develop their foraging skills (Chapter 6) and once fledglings are sufficiently satiated it may be better for them to invest in behaviours to develop their foraging skills (Thornton 2008a) rather than beg for more food (Chapter6). Finally, adult pied babblers are known to punish begging fledglings in order to partition care when brood overlap occurs (Raihani & Ridley 2008b). Fledgling begging may be kept from escalating by the risk of punishment from adults.

In this species, fledgling begging was unaffected by the begging behaviour of their siblings. Begging was therefore neither competitive nor cooperative. Pied babbler fledglings were not competing over a fixed amount of resources: my results reveal that adults increased their provisioning rates to accommodate higher levels of offspring demand. This is in direct contrast to models that predict a competitive response to sibling begging, as they assume the amount of resources available to offspring to be fixed (MacNair & Parker 1979; Godfray 1995; Rodríguez-Gironés 1999; Romano et al. 2012). Hence, under these models, begging escalation occurs as offspring seek to gain a share of limited resources. Biparental species have been shown to be flexible in their responsiveness to offspring solicitation (Thorogood et al. 2011), but the presence of helpers in cooperative breeding species, which may lower the cost of care per individual (Hatchwell 1999; Russell et al. 2007a; Russell et al. 2008; Meade et al. 2010), might mean that cooperative breeders are better placed than biparental species to increase provisioning level in response to increased offspring demand. Adults may also be able to increase their foraging effort in order to meet the increased demand of fledglings. For example, adult meerkats increase the amount of time they spend foraging when pup begging increases (Kunc et al. 2007). Future studies could investigate whether adult pied babblers increase the proportion of time spent foraging in response to experimentally elevated begging from fledglings.

Pied babbler care-givers appear to be able to tailor their allocation of resources to individual fledgling begging, provisioning each fledgling relative to its begging effort. Models of cooperative begging (Johnstone 2004) require asymmetry in competitive ability between broodmates, enabling dominant offspring to parasitize the begging effort of their siblings. However, I showed that adults apparently target their provisioning in response to individual increased demand. In this context, cooperative begging may be unprofitable because fledglings stand to gain limited provisioning benefits from the extra begging of their siblings. The mobile and dispersed nature of the fledgling environment means that individuals can distance themselves from competitors (McGowan & Woolfenden 1990; Langen 1996a) and are rarely competing for the attention of the same adult (Appendix 1), potentially enabling

them to reduce the impact of any existing competitive asymmetries. Also, because fledgling pied babblers accompany care-givers, they can provide on-going information about individual hunger, a situation that is very different to that of nestling birds: who have a short period of time to communicate with adults (Haskell 1994; Briskie et al. 1999; Manser & Avey 2000; McDonald et al. 2009). It may therefore be easier for pied babbler care-givers to make provisioning decisions based on offspring hunger and so target their provisioning to the fledglings that are begging the most. The dispersed distribution of fledglings combined with the fact that adult pied babblers, as in other species, predominantly feed the closest chick (Brotherton et al. 2001; Thompson & Ridley 2013) means that a system of cooperative begging, as described by Johnstone (2004), is unlikely to be profitable. Cooperative begging in a mobile system has been described for banded mongooses (Bell 2007), despite the fact that this begging system does not function in a parasitic way as modelled by Johnstone (2004). Bell (2007) proposes that the banded mongoose escort system, where individual pups follow specific adults for their period of dependence (Gilchrist 2004), reduces competition over provisioning enabling cooperation (Johnstone 2004). In contrast, the association system of pied babblers is very different, as fledglings frequently move between different care-givers (Thompson & Ridley 2013).

The provisioning rate received by control fledglings remained constant both when their sibling's begging was experimentally decreased (through supplemental feeding) and increased (through playbacks). Fledglings suffered no provisioning costs nor gained any provisioning benefits when their siblings' begging changed. There are two potential explanations for why adult provisioning to control fledglings was unaffected by experimental playbacks. Firstly, the overall provisioning level to the brood was flexible, with adults provisioning experimental fledglings in relation to their treatment while maintaining provisioning levels to control fledgling. Therefore, fledglings were not competing for a limited amount of resources. Secondly, the increases and decreases in provisioning were targeted to the experimental chick whose begging had been manipulated. The fact that control fledglings do not suffer a provisioning cost is likely to reduce the pay-off fledglings gain from escalating their own begging displays: it does not benefit an individual to increase

its begging when its sibling begs more, because they are not competing over a fixed amount of resources and so the provisioning that individual receives will not change. In addition, unlike the cooperatively begging banded mongoose (Bell 2007) babbler fledglings also gained no direct provisioning benefit from the elevated begging of their siblings. Fledglings also suffered no decrease in provisioning when the overall brood begging level decreased (Bell 2007). This combination of siblings suffering no provisioning costs or benefits suggests it is uneconomical for pied babbler fledglings to adjust their begging in response to their siblings.

In altricial birds, the act of fledging changes an offspring's environment with consequences for the pay-offs of begging and the allocation of resources: as an offspring's environment will influence the costs and benefits of behaviours (Kedar et al. 2000; Royle et al. 2002). Studies of begging behaviour have largely been confined to altricial nestling birds (Hudson & Trillmich 2007). However, there is a growing literature investigating the begging of mobile offspring (Smiseth & Moore 2002; Kunc et al. 2007; Bell 2008a; English et al. 2008; Madden et al. 2009b). The mobile nature of fledgling pied babblers means they inhabit an environment more akin to the dependent phase in social mammal species, such as meerkats and banded mongooses, than that of nestling birds. Pied babbler fledglings, meerkat and banded mongoose pups all beg and are provisioned whilst accompanying the foraging group (Gilchrist 2004; Hodge 2005; Thompson & Ridley 2013). However, in contrast to pied babbler fledglings, both meerkat and banded mongoose pups modify their begging behaviour relative to that of their littermates (Bell 2007; Madden et al. 2009b). The majority of ways that meerkat pups responded to their litter-mates would be described as cooperative: pups reduced their begging rate when litter begging level was artificially increased and decreased begging when close to other pups (Madden et al. 2009b). However, meerkat pups in larger litters had higher begging rates which fits with competitive begging theory (Madden et al. 2009b). On the other hand, banded mongoose pups use an exclusively cooperative begging signal, whereby the removal of pups induces an increase in begging in the remaining young in order to maintain the same level of provisioning (Bell 2007). Given the similarities between these three species systems of care, it is not obvious

why offspring's response to siblings' begging should be different. However, one potential explanation for the differences is in regards to relatedness and kin selection. Pied babblers fledglings are highly related (Nelson-Flower et al. 2011), with a much larger proportion of offspring being from the dominant pair than in meerkats (Griffin et al. 2003) or the communally breeding banded mongoose (De Luca & Ginsberg 2001). Therefore, in an evolutionary context, both fledglings and helpers can be confident of being highly related to one another and receiving indirect benefits (Hamilton 1963). Lower rates of relatedness and high rates of infanticide in meerkats (Young & Clutton-Brock 2006) and banded mongooses (Gilchrist 2006) may mean that pups are selected to conceal individual identity, reducing care-giver ability to discriminate between them and thus care-givers may have to use the begging of the whole litter to inform resource allocation. In addition, both meerkat and banded mongoose pups adjust their begging behaviour to their social context, increasing their begging rate when socially foraging with adults who provision at high rates (Bell 2008a; Bell 2008b; Madden et al. 2009c). Pied babbler fledglings have been shown to adjust their social foraging behaviour in relation to the likelihood that care-givers are going to provision them and so maximize the provisioning rate they receive (Thompson & Ridley 2013). However, it remains an area for further investigation to determine if fledglings adjust their begging behaviour in relation to an adult's propensity to provision.

There are two important to factors to note regarding this study. Firstly, the experimental manipulations carried out in this study were only short-term, and carried out in years with non-extreme levels of food abundance. It is possible that a long-term manipulation of fledgling demand, potentially achieved by artificially increasing begging rates over a series of days, would lead to different responses from both siblings and care-givers. Care-givers may be able to adjust their provisioning in the short-term, since short-term changes in offspring need are likely to be a common natural occurrence and are unlikely to carry long-term costs for care-givers. However, a long-term chronic increase in demand could result in adults being unable to maintain higher provisioning rates or becoming desensitized to fledgling begging (Thorogood et al. 2011; Riou et al. 2012). If adults were unable to adjust their provisioning rates then fledglings would be competing over a limited amount of resources,

and so it is likely that fledglings would alter their response to their siblings' begging effort in an attempt to maintain the level of feeding they receive (Royle et al. 2002). An extension of this study would be to conduct the same experiments in drought years, when resources are scarce and adults are less likely to be able to cope with increased fledgling demand. Secondly, only one aspect of fledgling begging was measured in this study: the proportion of time spent begging. Additional components of fledgling begging may have been affected by the begging behaviour of siblings, such as begging rate, call amplitude, peak frequency or bandwidth. It would be interesting if different elements of begging varied relative to sibling begging effort. However, how these aspects of begging respond to begging in siblings remains to be investigated.

The provisioning levels of adult pied babblers were flexible: when one fledgling's begging increased adults were able to target their increased provisioning to that fledgling while maintaining provisioning rates to its' siblings. Therefore, pied babbler fledgling begging influenced both the amount of food delivered to the brood, and the allocation of that food (Johnstone 2004). The influence fledgling begging has on the overall provisioning rate and allocation means that fledglings suffered no direct cost (lost provisioning) or direct benefit (additional provisioning) from elevated or reduced begging by their siblings. This, combined with the dispersed nature of fledglings, is likely to be the reason that begging behaviour in pied babblers was independent of sibling begging. These results suggest that care-givers may exert more control over provisioning than fledglings in this system (Johnstone 2004) and that begging in pied babbler fledglings may be a reliable signal of offspring hunger (Godfray 1995).

4.6 Chapter 4 Appendix

The influence of siblings on pied babbler fledgling begging

Candidate models tested

For tables S4.1-S4.8: Deviance= -2log-likelihood output of each model; *K*= the number of parameters tested in each model; AICc= Akaike's information criterion for small data sets; ΔAICc= the models AICc minus the minimum AICc among candidate models. For each candidate model: Basic= basic model with no predictor terms, only the constant, the random terms and residual variance (σ^2); Fage = fledgling age (days); Fsex = fledgling sex (female or male); F*W = the interaction between focal (before or after) and number of supplemental worms fed (0, 1, 5 or 10); F*Pb = the interaction between focal (before or after) and the playback begging rate (0, 12, 24 or 36); Anum = number of adults in the group; Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio. All models with ΔAICc <5 are in bold.

Table S4.1: Effects of feeding on experimental fledglings' begging

Model	Deviance	*K*	AICc	ΔAICc
F*W + Fage	**570.02**	**10**	**593.96**	**0**
F*W	**572.45**	**9**	**594.05**	**0.1**
F*W + Fage + Fnum	**569.08**	**11**	**595.39**	**1.43**
F*W + Fage + ADFL	**596.15**	**11**	**595.46**	**1.51**
F*W + Fnum	**571.54**	**10**	**595.48**	**1.52**
F*W + ADFL	**571.57**	**10**	**595.51**	**1.55**
F*W + Fage + Anum	**569.68**	**11**	**595.99**	**2.03**
F*W + Anum	**572.24**	**10**	**596.19**	**2.23**
F*W + Fsex	**572.33**	**11**	**596.27**	**2.31**
F*W + Fage + Fsex	**569.97**	**12**	**596.28**	**2.32**
F*W + Fage*Fsex	**570**	**15**	**596.31**	**2.35**
F*W + Fsex + Fnum	**571.22**	**12**	**597.54**	**3.58**
F*W + Fsex + ADFL	**571.23**	**12**	**597.54**	**3.59**
F*W + Fsex + Anum	**572.15**	**12**	**598.46**	**4.51**
Basic	664.53	3	670.7	76.74
Fnum	662.92	4	671.2	77.24
Anum + Fnum	661.38	5	671.8	77.84
Anum	663.6	4	671.88	77.92
ADFL	663.78	4	672.06	78.1
Fage	664.41	4	672.69	78.73
Fsex	664.53	5	672.81	78.85
Fage + Fnum	662.76	5	673.18	79.22
Fsex + Fnum	662.79	6	673.22	79.26
Fage + Anum	663.43	5	673.85	79.9
Fsex + Anum	663.6	6	674.02	80.06
Fage + ADFL	663.66	5	674.08	80.12
Fsex + ADFL	663.73	6	674.15	80.19
Fage*Fsex	664.36	6	674.78	80.82

Fage + Fsex	664.41	6	674.83	80.88
Fage + Fsex + Fnum	662.66	7	675.25	81.3
Fage + Fsex + Anum	663.43	7	676.03	82.07
Fage + Fsex + ADFL	663.62	7	676.21	82.26

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.2: Effects of feeding on provisioning to experimental fledglings

Model	Deviance	*K*	AICc	Δ AICc
F*W + Fage	**-241.96**	**10**	**-218.02**	**0**
F*W + Fage + ADFL	**-242.81**	**11**	**-216.5**	**1.52**
F*W + Fage + Fnum	**-242.34**	**11**	**-216.03**	**1.99**
F*W + Fage + Fsex	**-242.1**	**12**	**-215.79**	**2.23**
F*W + Fage + Anum	**-242.03**	**11**	**-215.71**	**2.31**
F*W + Fage*Fsex	**-241.97**	**15**	**-215.66**	**2.36**
F*W	-224.02	9	-204.42	13.6
F*W + ADFL	-224.79	10	-200.85	17.17
F*W + Fnum	-224.3	10	-200.36	17.66
F*W + Anum	-224.21	10	-200.27	17.75
F*W + Fsex	-224.02	11	-200.08	17.94
F*W + Fsex + ADFL	-224.84	12	-198.53	19.5
F*W + Fsex + Fnum	-224.32	12	-198.01	20.01
F*W + Fsex + Anum	-224.22	12	-197.9	20.12
Fage	-204.12	4	-195.84	22.18
Fage + Fnum	-205.14	5	-194.72	23.31
Fage + ADFL	-204.91	5	-194.49	23.53
Fage + Fsex	-204.48	6	-194.06	23.96
Fage*Fsex	-204.29	6	-193.87	24.15
Fage + Anum	-204.27	5	-193.85	24.17
Fage + Fsex + Fnum	-205.29	7	-192.69	25.33
Fage + Fsex + ADFL	-205.1	7	-192.5	25.52
Fage + Fsex + Anum	-204.67	7	-192.07	25.95
Basic	-193.21	3	-187.04	30.98
ADFL	-194.1	4	-185.82	32.2
Fnum	-194.02	4	-185.74	32.28
Fsex	-193.28	5	-185	33.02
Anum	-193.21	4	-184.93	33.09
Fsex + ADFL	-194.1	6	-183.68	34.34
Anum + Fnum	-194.06	5	-183.63	34.39
Fsex + Fnum	-194.02	6	-183.6	34.43
Fsex + Anum	-193.28	6	-182.86	35.16

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.3: Effect of playbacks on provisioning to experimental fledglings

Model	Deviance	*K*	AICc	Δ AICc
F*Pb + Fage	**-209.25**	**10**	**-185.22**	**0**
F*Pb + Fage + ADFL	**-210.66**	**11**	**-184.24**	**0.99**
F*Pb + Fage*Fsex	**-209.82**	**15**	**-183.4**	**1.82**
F*Pb + Fage + Fsex	**-209.54**	**12**	**-183.12**	**2.1**
F*Pb + Fage + Anum	**-209.53**	**11**	**-183.12**	**2.11**
F*Pb + Fage + Fnum	**-209.25**	**11**	**-182.84**	**2.39**
F*Pb	-197.39	9	-175.71	9.51
F*Pb + ADFL	-197.78	10	-173.74	11.48
F*Pb + Fsex	-197.72	11	-173.69	11.54
F*Pb + Anum	-197.42	10	-173.38	11.84
F*Pb + Fnum	-197.39	10	-173.36	11.86
F*Pb + Fsex + ADFL	-198.09	12	-171.67	13.55
F*Pb + Fsex + Anum	-197.75	12	-171.33	13.89
F*Pb + Fsex + Fnum	-197.73	12	-171.31	13.92
Fage + ADFL	-167.1	5	-156.66	28.56
Fage	-164.7	4	-156.41	28.82
Fage*Fsex	-166.8	6	-156.35	28.87
Fage + Fsex + ADFL	-168.66	7	-156.03	29.19
Fage + Fsex	-166.34	6	-155.9	29.33
Fage + Anum	-165.73	5	-155.29	29.94
Fage + Fsex + Anum	-167.24	7	-154.62	30.61
Fage + Fnum	-164.87	5	-154.43	30.8
Fage + Fsex + Fnum	-166.4	7	-153.78	31.44
Basic	-156.89	3	-150.72	34.51
Fsex	-158.46	5	-150.17	35.06
ADFL	-157.92	4	-149.62	35.6
Fsex + ADFL	-159.4	6	-148.96	36.27
Anum	-157.03	4	-148.73	36.49
Fnum	-157	4	-148.71	36.52
Fsex + Anum	-158.54	6	-148.1	37.13
Fsex + Fnum	-158.49	6	-148.05	37.17
Anum + Fnum	-157.07	5	-146.63	38.6

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.4: Effects of feeding on control fledglings' begging

Model	Deviance	*K*	AICc	Δ AICc
Fsex	**218.34**	**5**	**227.19**	**0**
Basic	**221.01**	**3**	**227.51**	**0.32**
Fage + Fsex	**217.32**	**6**	**228.63**	**1.44**
Fage	**220.25**	**4**	**229.11**	**1.91**
Fsex + Fnum	**218.25**	**6**	**229.56**	**2.37**
Fsex + Anum	**218.29**	**6**	**229.59**	**2.4**
Fsex + ADFL	**218.32**	**6**	**229.63**	**2.44**
Anum	**220.92**	**4**	**229.77**	**2.58**
Fnum	**220.93**	**4**	**229.78**	**2.59**
ADFL	**221.01**	**4**	**229.86**	**2.66**
Fage*Fsex	**218.8**	**6**	**230.11**	**2.91**
Fage + Fsex + ADFL	**217.19**	**7**	**231.05**	**3.86**
Fage + Fsex + Fnum	**217.23**	**7**	**231.1**	**3.9**
Fage + Fsex + Anum	**217.32**	**7**	**231.19**	**4**
Fage + Fnum	**220.14**	**5**	**231.45**	**4.26**
Fage + ADFL	**220.16**	**5**	**231.46**	**4.27**
Fage + Anum	**220.24**	**5**	**231.54**	**4.35**
Fage + Fnum	**220.78**	**5**	**232.08**	**4.89**
F*W + Fsex	216.26	11	238.55	11.36
F*W	219.52	9	238.87	11.68
F*W + Fage + Fsex	214.26	12	239.62	12.43
F*W + Fage	218.18	10	240.46	13.27
F*W + Fsex + Anum	215.89	12	241.25	14.06
F*W + Anum	219.11	10	241.4	14.21
F*W + Fsex + ADFL	216.09	12	241.45	14.26
F*W + Fsex + Fnum	216.25	12	241.62	14.42
F*W + Fage*Fsex	216.26	15	241.63	14.44
F*W + ADFL	219.39	10	241.67	14.48
F*W + Fnum	219.52	10	241.8	14.61
F*W + Fage + Anum	217.98	11	243.34	16.15
F*W + Fage + ADFL	218.16	11	243.52	16.33
F*W + Fage + Fnum	218.18	11	243.54	16.35

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.5: Effect of playbacks on control fledglings' begging

Model	Deviance	*K*	AICc	Δ AICc
Basic	**282.24**	**3**	**288.61**	**0**
Anum	**280.15**	**4**	**288.79**	**0.18**
ADFL	**280.38**	**4**	**289.02**	**0.4**
Fnum	**280.65**	**4**	**289.28**	**0.67**
Anum + Fnum	**279.21**	**5**	**290.17**	**1.56**
Fage	**281.79**	**4**	**290.42**	**1.81**
Fsex	**282.2**	**5**	**290.83**	**2.22**
Fsex + Anum	**280.08**	**6**	**291.05**	**2.44**
Fage + Anum	**280.13**	**5**	**291.09**	**2.48**
Fsex + ADFL	**280.18**	**6**	**291.15**	**2.54**
Fage + ADFL	**280.36**	**5**	**291.33**	**2.71**
Fsex + Fnum	**280.37**	**6**	**291.34**	**2.73**
Fage + Fnum	**280.51**	**5**	**291.47**	**2.86**
Fage*Fsex	**281.58**	**6**	**292.55**	**3.94**
Fage + Fsex	**281.72**	**6**	**292.69**	**4.08**
Fage + Fsex + Anum	**280.05**	**7**	**293.42**	**4.81**
Fage + Fsex + ADFL	**280.15**	**7**	**293.53**	**4.92**
Fage + Fsex + Fnum	**280.21**	**7**	**293.59**	**4.98**
F*Pb	275.38	9	293.82	5.21
F*Pb + Anum	273.48	10	294.58	5.97
F*Pb + ADFL	273.77	10	294.88	6.27
F*Pb + Fnum	273.97	10	295.08	6.47
F*Pb + Fage	274.93	10	296.04	7.43
F*Pb + Fsex	275.26	11	296.36	7.75
F*Pb + Fsex + Anum	273.29	12	297.15	8.54
F*Pb + Fage + Anum	273.44	11	297.3	8.69
F*Pb + Fsex + ADFL	273.45	12	297.31	8.7
F*Pb + Fsex + Fnum	273.58	12	297.44	8.83
F*Pb + Fage + ADFL	273.73	11	297.58	8.97
F*Pb + Fage + Fnum	273.82	11	297.68	9.07
F*Pb + Fage*Fsex	274.52	15	298.38	9.77
F*Pb + Fage + Fsex	274.76	12	298.62	10.01

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.6: Effects of playback on experimental fledglings' begging

Model	Deviance	*K*	AICc	Δ AICc
Fage	**576.07**	**4**	**584.36**	**0**
Fage + Fnum	**574**	**5**	**584.44**	**0.07**
Basic	**578.66**	**3**	**584.83**	**0.47**
Fnum	**576.88**	**4**	**585.17**	**0.81**
Fage*Fsex	**575.24**	**6**	**585.69**	**1.32**
Fage + Fsex	**575.75**	**6**	**586.19**	**1.82**
Fage + ADFL	**575.76**	**5**	**586.2**	**1.84**
Fage + Anum	**575.94**	**5**	**586.39**	**2.02**
Fage + Fsex + Fnum	**573.81**	**7**	**586.43**	**2.07**
Fsex	**578.35**	**5**	**586.64**	**2.27**
ADFL	**578.53**	**4**	**586.82**	**2.46**
Anum	**578.63**	**4**	**586.92**	**2.56**
Anum + Fnum	**576.56**	**5**	**587.01**	**2.64**
Fsex + Fnum	**576.69**	**6**	**587.13**	**2.77**
Fage + Fsex + ADFL	**575.46**	**7**	**588.08**	**3.72**
Fage + Fsex + Anum	**575.65**	**7**	**588.27**	**3.91**
Fsex + ADFL	**578.23**	**6**	**588.67**	**4.31**
Fsex + Anum	**578.33**	**6**	**588.77**	**4.41**
F*Pb + Fage + Fnum	566.87	11	593.29	8.92
F*Pb + Fage	569.78	10	593.81	9.45
F*Pb + Fnum	569.87	10	593.9	9.54
F*Pb	572.32	9	594	9.63
F*Pb + Fage + ADFL	568.93	11	595.35	10.99
F*Pb + Fage*Fsex	569.08	15	595.5	11.14
F*Pb + Fage + Anum	569.31	11	595.73	11.36
F*Pb + ADFL	571.88	10	595.91	11.55
F*Pb + Fage + Fsex	569.54	12	595.95	11.59
F*Pb + Fsex	572.07	11	596.1	11.73
F*Pb + Fsex + Fnum	569.73	12	596.14	11.78
F*Pb + Anum	572.12	10	596.15	11.79
F*Pb + Fsex + ADFL	571.64	12	598.05	13.69
F*Pb + Fsex + Anum'	571.9	12	598.32	13.95

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.7: Effects of feeding on provisioning to control fledglings

Model	Deviance	*K*	AICc	Δ AICc
Fage + Fnum	**-81.86**	**5**	**-70.56**	**0**
Fage	**-78.71**	**4**	**-69.86**	**0.7**
Fage + Fsex + Fnum	**-82.54**	**7**	**-68.67**	**1.88**
F*W + Fage + Fnum	**-94.01**	**11**	**-68.64**	**1.92**
Fage*Fsex	**-79.92**	**6**	**-68.62**	**1.94**
Fage + Fsex	**-79.3**	**6**	**-68**	**2.56**
Basic	**-74.16**	**3**	**-67.66**	**2.9**
Fage + Anum	**-78.92**	**5**	**-67.62**	**2.94**
Fage + ADFL	**-78.77**	**5**	**-67.46**	**3.1**
Fnum	**-76.29**	**4**	**-67.44**	**3.12**
Anum + Fnum	**-77.55**	**5**	**-66.24**	**4.31**
Anum	**-74.75**	**4**	**-65.9**	**4.66**
Fsex	**-74.57**	**5**	**-65.72**	**4.84**
F*W + Fnum	**-87.94**	**10**	**-65.65**	**4.9**
Fage + Fsex + Anum	**-79.51**	**7**	**-65.64**	**4.91**
Fage + Fsex + ADFL	-79.36	7	-65.5	5.06
Fsex + Fnum	-76.79	6	-65.49	5.07
ADFL	-74.21	4	-65.36	5.19
F*W + Fage	-86.81	10	-64.53	6.03
Fsex + Anum	-75.15	6	-63.85	6.71
Fsex + ADFL	-74.62	6	-63.31	7.24
F*W	-82.24	9	-62.89	7.66
F*W + Fage*Fsex	-88.23	15	-62.87	7.69
F*W + Fsex + Fnum	-88.2	12	-62.83	7.72
F*W + Fage + ADFL	-87.8	11	-62.43	8.13
F*W + Fage + Fsex	-87.24	12	-61.87	8.68
F*W + Fage + Anum	-86.83	11	-61.46	9.1
F*W + ADFL	-82.55	10	-60.26	10.29
F*W + Fsex	-82.46	11	-60.18	10.38
F*W + Anum	-82.36	10	-60.08	10.48
F*W + Fsex + ADFL	-82.76	12	-57.39	13.16
F*W + Fsex + Anum	-82.58	12	-57.22	13.34

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.8: Effect of playbacks on provisioning to control fledglings

Model	Deviance	*K*	AICc	Δ AICc
Fage + ADFL	**-116.88**	**5**	**-105.91**	**0**
Fage + Fnum	**-116.33**	**5**	**-105.36**	**0.55**
Fage	**-113.64**	**4**	**-105.01**	**0.9**
Fage + Anum	**-115.7**	**5**	**-104.73**	**1.18**
Fage + Fsex + ADFL	**-117.51**	**7**	**-104.14**	**1.77**
Fage + Fsex + Fnum	**-117.39**	**7**	**-104.01**	**1.9**
Fage*Fsex	**-114.14**	**6**	**-103.17**	**2.74**
Fage + Fsex	**-114.07**	**6**	**-103.1**	**2.81**
Fage + Fsex + Anum	**-116.04**	**7**	**-102.66**	**3.25**
ADFL	**-111.19**	**4**	**-102.56**	**3.35**
Anum + Fnum	**-112.05**	**5**	**-101.08**	**4.83**
Fsex + ADFL	-111.58	6	-100.61	5.3
Anum	-109.19	4	-100.56	5.35
Fnum	-108.74	4	-100.11	5.8
F*Pb + Fage + Fnum	-123.2	11	-99.34	6.57
Fsex + Fnum	-109.5	6	-98.53	7.38
F*Pb + Fage + ADFL	-122.35	11	-98.49	7.42
Fsex + Anum	-109.28	6	-98.31	7.6
F*Pb + Fage	-119.05	10	-97.95	7.96
Basic	-103.77	3	-97.4	8.51
F*Pb + Fage + Anum	-120.76	11	-96.9	9.01
F*Pb + Fage*Fsex	-119.19	15	-95.33	10.58
F*Pb + ADFL	-116.4	10	-95.29	10.62
F*Pb + Fage + Fsex	-119.13	12	-95.27	10.64
Fsex	-103.87	5	-95.23	10.68
F*Pb + Fnum	-115.82	10	-94.71	11.2
F*Pb + Anum	-113.73	10	-92.62	13.29
F*Pb + Fsex + ADFL	-116.46	12	-92.6	13.31
F*Pb + Fsex + Fnum	-116.11	12	-92.25	13.66
F*Pb	-108.83	9	-90.39	15.52
F*Pb + Fsex + Anum	-113.73	12	-89.87	16.04
F*Pb + Fsex	-108.83	11	-87.73	18.19

All LMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data.

Table S4.9: Predictor terms for models investigating effects on fledgling begging and provisioning to fledglings in the feeding and playback experiments

Terms	Feeding experiment				Playback experiment			
	Begging (%)		Provisioning rate (g.min^{-1})		Begging (%)		Provisioning rate (g.min^{-1})	
	Exp.	Con.	Exp.	Con.	Exp.	Con.	Exp.	Con.
Fage	**0.499**	0.339	**0.999**	**0.776**	0.581	0.252	**0.992**	**0.892**
Fsex	0.233	0.551	0.228	0.303	0.32	0.248	0.249	0.32
F*W	**1**	0.003	**1**	0.129	*	*	*	*
F*Pb	*	*	*	*	0.009	0.048	**1**	0.022
Anum	0.135	0.165	0.113	0.117	0.157	0.298	0.116	0.185
Fnum	0.19	0.168	0.132	0.46	0.339	0.254	0.101	0.266
ADFL	0.186	0.149	0.168	0.084	0.13	0.212	0.202	0.333

Predictor weights for the all variables investigated in LMMs. Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable (Symonds & Moussalli 2011). Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011). Exp. = experimentally manipulated fledglings: supplementally fed meal worms; begging rate artificially increased with a playback. Con. = control fledglings, who were not manipulated. Variables not investigated in the models are represented by *.All variables deemed to be important are in bold.

Chapter 5

The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis

This work has been published as Thompson, A.M., Raihani, N.J., Hockey, P.A.R, Britton, A., Finch, F.M. & Ridley, A.R. (2013) *Proceedings of the Royal Society B* 280, 20130558. A.R. Ridley, N.J. Raihani and P.A.R. Hockey assisted in discussion and commented on drafts of the manuscript. A. Britton and F.M. Finch assisted with data collection. I designed all the data collection protocols, analysed all the data and wrote the paper. The published paper has been edited to fit in with the structure of this thesis.

The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis

5.1 Abstract

One theory to explain the existence of conspicuous solicitation is that it is a way for young to 'blackmail' care-givers into provisioning them, by threatening their own destruction. Fledgling birds offer a unique opportunity to investigate the 'blackmail theory', as their mobility enables them to influence the predation risk they face. I investigated a novel solicitation behaviour in fledgling pied babblers, where fledglings use their location to influence provisioning rates. I show that fledglings face a trade-off: the ground is a much more profitable location in terms of provisioning rate from adult care-givers, but they are at greater risk from predators due to their limited flying ability and slow response to alarm calls. Young babbler fledglings move to the ground when hungry, signalling their state, and this stimulates adults to increase their provisioning rates. Once satiated, fledglings return to the safety of cover. By experimentally increasing terrestrial predation risk, I found that adults increased their provisioning rate to terrestrial but not arboreal fledglings. Thus, by moving to a riskier location, fledglings revealed their need and were able to manipulate adults to achieve higher provisioning rates. These results provide support for the 'blackmail theory'.

5.2 Introduction

Altricial young are dependent on adults to provide them with the necessary nutrition for growth and development (Smiseth et al. 2012). The nutritional needs of altricial young may be cryptic and difficult for care-givers to determine (Godfray 1991; Godfray 1995), hence both care-givers and young will benefit from young communicating their need. Previous research has revealed that conspicuous solicitation behaviours have evolved in many species to enable dependent young to signal to and extract resources from care-givers (reviewed in Mock et al. 2011). However, due to genetic asymmetries caused by sexual reproduction, theory predicts different optimal levels of investment for parents and offspring (Trivers 1974). Parents and offspring are therefore predicted to 'disagree' over provisioning behaviour; a concept known as parent-offspring conflict (POC). POC has been

the subject of much theoretical and empirical research in a variety of taxa (reviewed in (Kilner & Johnstone 1997; Mock et al. 2011)). Trivers (1974) originally hypothesized that offspring use solicitation behaviours to manipulate parents into provisioning them at a higher level than is optimal for the parents. Zahavi (1977b) expanded on this concept by proposing that predation risk shapes parent-offspring interactions, suggesting that vocal begging is an attempt by offspring to 'blackmail' parents into provisioning them by the threat of their own destruction. Here, I empirically test Zahavi's theory in a novel social context.

When the production of solicitation displays imposes a cost on the signaller, the cost of the signal means the signal is more likely to be honest (Zahavi 1975; Godfray 1991). Two main costs have been put forward for solicitation behaviours (Godfray 1991): energy expenditure and predation risk. The metabolic costs of begging have been investigated, with mixed results (Leech & Leonard 1996; McCarty 1996). In contrast, predation risk has been shown to be a greater cost associated with begging: Haskell (1994) showed that nestling birds suffer a real risk of predation due to begging, suggesting that predation risk may promote honesty in nestling begging signals (Johnstone 1996b).

The majority of theoretical and empirical studies of avian solicitation and POC have focused on nestlings (Kunc et al. 2007), due to the difficulties in observing fledglings (Suedkamp Wells et al. 2007). However, the nestling and fledgling environments are qualitatively different: nestlings are in a fixed location, in close proximity to their siblings and have to wait for adults to return and provision them. In contrast, fledglings are mobile and able to follow adults to solicit food directly (Thompson & Ridley 2013). Fledgling predation risks are therefore different to those of nestlings, resulting in different mortality rates according to developmental stage (Magrath et al. 2006; Ridley & van den Heuvel 2012). During the nestling phase, offspring are a fixed source of noise that gradually gets louder during the nestling period (Leonard & Horn 2006), making them more conspicuous to predators (Haskell 1994). In contrast, the mobility of fledglings means they are no longer a fixed source of noise, but can move in a three-dimensional environment (Manser & Avey 2000;

Magrath et al. 2010), where predation risk can vary depending on their location (Lima & Dill 1990).

The vulnerability of offspring to predation will depend critically on their ability to evaluate and respond to predation risk. The young of many species react to predation risk either by responding to adult alarm calls (Davies et al. 2004; Magrath et al. 2006) or by assessing predation risk independently of cues/warnings from adults (reviewed in (Magrath et al. 2010)). For example, nestling white-browed scrubwrens (*Sericornis frontalis*) use the sound of their major predator (pied currawong *Strepera graculina*) walking in leaf litter to assess predation risk and stop begging when they hear this noise (Magrath et al. 2007; Haff & Magrath 2010). Nestling common grackles (*Quiscalus versicolr*) (Schaller & Emlen 1961) and moustached warblers (*Acrocephalus melanopogon*) (Kleindorfer et al. 1996), can detect predators using visual stimuli. However, the response to predation risk is often poor or inappropriate in naïve young (Ridley & Child 2009), because perception of risk may often be dependent on past experience (Ydenberg & Dill 1986). Offspring response to predators can also be limited by developmental constraints, such as limited physical capacity to evade predators (Espmark & Langvatn 1985).

All animals face a trade-off between food intake and anti-predation behaviour (Ydenberg & Dill 1986). When offspring are directly dependent upon adult care-givers, those adults can be viewed as a food source or foraging patch. Fledglings may therefore face a trade-off between either following adult caregivers or remaining in safer, but less profitable locations, such as under the cover of trees or bushes (Ridley et al. 2013). This trade-off is particularly relevant for terrestrially foraging birds, whose main escape from predators is to flee to cover in bushes and trees (Lima & Dill 1990; Ridley et al. 2013). If energetic rewards are greatest when following care-givers in locations of higher predation risk (Holomuzki 1986), fledglings face a trade-off between maximizing their growth rates and maximizing their survival. Therefore, I predict that the level of risk that fledglings are willing to tolerate will depend critically on their hunger level: hungrier fledglings should be willing to accept higher predation risk to achieve greater amounts of provisioning.

Pied babblers fledge their young at a very immature stage – young are unable to fly for up to a week post-fledging and take a long time to develop adult-like mobility (Raihani & Ridley 2007b). This poor mobility has the potential to put them at greater risk from predators compared to adult babblers, offering a unique opportunity to investigate post-fledgling conflict over provisioning. Here, I investigate whether hungrier fledglings move to riskier locations to increase the amount of provisioning they receive from adults, presenting the opportunity to test Zahavi's (1977b) prediction that begging behaviour will be most effective in areas with high predation risk. To investigate the relationship between offspring solicitation, predation risk and adult provisioning, the threat of predation needs to be altered (Johnstone 1996b; Lummaa et al. 1998). Through observations and experimental manipulations of predation risk, I determined a) whether terrestrially located fledglings are at higher risk of predation; b) the optimal location for fledglings (terrestrial or arboreal) in terms of adult provisioning rates; and c) whether changes in predation risk cause adults to change their behaviour toward fledglings.

5.3 Methods

5.3.1 *Study site and species*

This study investigated adult-fledgling interactions in 14 groups of pied babblers in the southern Kalahari Desert at the Kuruman River Reserve, between November 2009 and March 2012. Pied babblers are predominantly terrestrial foragers, spending more than 95% of their foraging time on the ground (Ridley & Raihani 2007b). Young are unable to fly for up to a week post-fledging and are dependent upon adults for food for several months (Ridley & Raihani 2007a). During the post-fledging dependent phase, fledglings actively follow and beg for food from foraging adults (Thompson & Ridley 2013). See Chapter 2 for further details of the study population and the natural history of pied babblers. Both aerial and terrestrial predators are present at the study site; see Chapter 2 for a full predator list.

5.3.2 *Data collection*

5.3.2.1 *Behavioural data*

General behavioural data (here after '*adlib*') were collected using the *ad libitum* method (Altmann 1974). The behaviours recorded included: feeding events (identity of adult and chick, as well as food type and size), the location of the fledglings (ground or tree), and the duration (seconds) of all lead calls given by adults (Raihani & Ridley 2007a). Food item sizes and weights were calculated using the same methods as Ridley & Raihani (2007a). Lead calls are used by adults to move fledglings from one location to another and to move them away from danger (Raihani & Ridley 2007a). Lead call behaviour was deemed to have ceased when adults stopped emitting lead calls. Over 208 hours of field observations were carried out, encompassing 3177 feeding events. All *adlib* and focal data (see below) were recorded on a Palm T|X handheld PDA (Palm, Inc; Sunnydale, CA, USA).

5.3.2.2 *Response to alarm-call experiment*

To determine the speed of fledgling response to alarm calls, as a proxy for their vulnerability to predation, intense predator were simulated interactions by playing back pied babbler mobbing calls. Playbacks were created from recordings of natural mobbing events towards slender mongoose, made 10-15 m from the mobbing event. All sound was recorded using a RØDE™ NTG-2 shotgun microphone (RØDE microphones, Silverwater, NSW, Australia; frequency response 20-20,000 Hz ± 2 dB) onto a Microtrack II digital sound recorder (M-Audio™, Irwindale, CA, USA; frequency response 20-20'000 Hz ± 0.5 dB). Playbacks were created using Raven Pro 1.3© (Cornell Lab of Ornithology, Ithaca, NY, USA) and normalized to levels appropriate for the experiment. All playbacks were group-specific to avoid the group responding to the playback as if it were a neighbouring group. Playbacks were normalized to 85 dB and cut to 11 seconds long, to simulate natural mobbing alarms. Playbacks were conducted 10 m from the foraging group and only when at least one fledgling was located on the ground. To avoid groups habituating to playbacks, each playback was used only once and the gap between experiments at each group was one week. Playbacks were only conducted if the last major behavioural disturbance (predator alarm or inter-group-interaction) was more than 30 minutes before. The response recorded

was movement to cover (as defined by Ridley et al. (2013)), as this is the normal response to this type of alarm call. The response time to the playback by the focal fledgling and the nearest adult (less than 1 m) to them was recorded (seconds), along with the distance of the fledgling from cover (m).

5.3.2.3 *Feeding experiment*

To determine how hunger affected the location of fledglings I compared their behaviour before and after supplementary feeding. All data (27 fledglings from 12 groups) were collected while offspring were dependent upon adult care-givers for food (age range 31-84 days post-hatching). I used detailed focal observations (Altmann 1974) on individual fledglings lasting 20 minutes, during which all foraging events, begging events, feeding events (identity of feeder, and prey item type and size), lead calls (identity of caller, duration and context), and location (ground or tree) were recorded. A control focal observation was conducted on each fledgling, the fledgling was then fed 10 meal worms (approximately 4.5 g), and then a second 20-minute focal observation was carried out. The ~4.5g provided as supplementary food thus amounted to approximately 2.5 times the biomass a fledgling would normally consume on average per 20 minutes (1.68 ± 0.059 g S.E., range 0.0-6.4 g), constituting biomass likely to satiate the fledgling. Focal observations were not carried out during inter-group-interactions or immediately after major predator alarms, and focals were terminated if one of these events occurred after the focal had started. Data collection was paused when the bird was obscured from view and resumed when the bird was again in clear view. If the break in observation was longer than 5 minutes the focal observation was aborted. To account for any temporal effects, controls were also carried out (16 fledglings from 10 groups; age range 23-75 days post-hatching). The controls used the same methods as detailed above, except without supplementary feeding between focal observations.

5.3.2.4 *Predator perception experiment*

To determine whether an increase in perceived predation risk affected how adult pied babblers behaved toward fledglings, the quantity of heterospecific alarm calls that the group overheard was manipulated (similar to the technique used in previous studies (Bell et

al. 2009; Ridley et al. 2010)). Recordings were made of natural mobbing events on slender mongoose by Cape glossy-starlings (*Lamprotornis nitens*) and white-browed sparrow-weavers (*Plocepasser mahali*), co-occurring heterospecific species. Using these recordings I created experimental playbacks, normalized to 75 dB to mimic the volume of heterospecific alarm calls occurring in the *vicinity* of the group. Experimental playbacks comprised two 15-second bouts of mobbing separated by a 10 s bout of background noise. Control playbacks consisted of two 15 s bouts of contact calls (from the same heterospecific species) interspersed with 10 s of background noise. Six experimental and control exemplars were created. Experimental and control playbacks were paired and conducted on consecutive days, with the order randomized: individual experimental and control playbacks were never paired more than once. *Adlib* data were collected on each babbler group for 60 minutes. The first 30 minutes were the control for each treatment, and in the second 30 minutes a playback was conducted once every 10 minutes to simulate either an increased predation risk (experimental playback) or a continuation of the same level of risk (control playback). Playbacks were carried out 10 m from the foraging group. All experiments were conducted on 30 day old (~ two weeks post-fledging) fledglings, to control for age. This age was chosen because fledglings start coming to the ground more frequently, yet are still poor fliers with slow alarm call response (Raihani & Ridley 2007a).

5.3.3 *Statistical analyses*

All statistical analyses were conducted using GenStat 14th Edition (VSN International, Rothamstead, UK). Linear mixed models (LMMs) were used to assess (i) the difference in speed of response to alarm calls between adult and fledglings, (ii) provisioning rate to fledglings and (iii) proportion of time fledglings spent on the ground. I created a series of linear mixed models (LMMs) with normal distributions and identity link functions to investigate the response terms of interest. The effects of fixed terms were considered using maximum-likelihood estimation, and random terms were included to account for the potential influence of repeated measures. Model selection was carried out by using Akaike's Information Criterion for small datasets (AICc) (Hurvich & Tsai 1989) as the model selection criteria (Burnham & Anderson 2002; Burnham et al. 2011). A set of models to investigate *a*

priori hypotheses and a basic model that contained only the constant, random terms and residual variance were created. Co-linearity was checked for all explanatory terms and correlated terms were never included in the same model. The models were then ranked in order of their AICc values: models with lower AICc values were considered to have more explanatory power. Overall the model with the highest Akaike weight (w_i) and lowest AICc value was considered the best model, but all models within ΔAICc <5 were considered to have at least some support (Burnham & Anderson 2002). When more than one model appeared to have some support (i.e. ΔAICc <5), the importance of explanatory terms was evaluated by calculating the predictor weight (Symonds & Moussalli 2011) for each term. Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable (Symonds & Moussalli 2011). Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011). Here, I report the effect size and Wald statistic (χ^2) for predictor variables included in the most parsimonious model of those I considered in each analysis.

Paired analyses were carried out on paired experimental data to investigate: (1) The effect of hunger on the amount of time that fledglings spent on the ground and; (2) the effect of perceived predation risk on a) the percentage of time fledglings spent on the ground; b) the provisioning rate to terrestrially located fledglings; c) the provisioning rate to arboreally located fledglings and d) the proportion of time that adults spent giving lead calls to terrestrially located fledglings.

Tests for normality were conducted on all data. If data were non-normally distributed they were transformed: proportional data were arcsine-square-root transformed and non-proportional data were $\log_{10}$ or square-root transformed to achieve normality. If transformation did not result in a normal distribution, non-parametric tests were performed.

5.4 Results

5.4.1 *Fledgling response to alarm calls*

The response of fledglings to the alarm calls of adult group members was initially poor, with a large difference between adult and fledgling response time (mean response times: fledglings 12.6 sec (± 1.3 S.E.), adults 3.7 sec (± 0.3 S.E.)). As fledglings aged their response times to alarm calls increasingly converged on those of adults (Table 5.1; LMM effect -0.013 ± 0.003, χ^2 = 25.65; Figure. 5.1). The number of adults in the group also affected the alarm call response, with fledglings having a slower response in groups with more adults (Table 5.1; LMM effect 0.167 ± 0.051, χ^2 = 10.57). More than one model had ΔAICc <5; using predictor weights fledgling age and group size were the most important predictors of fledgling response time (Chapter 5 Appendix Table S5.4). For a list of all candidate models tested see Chapter 5 Appendix Table S5.1.

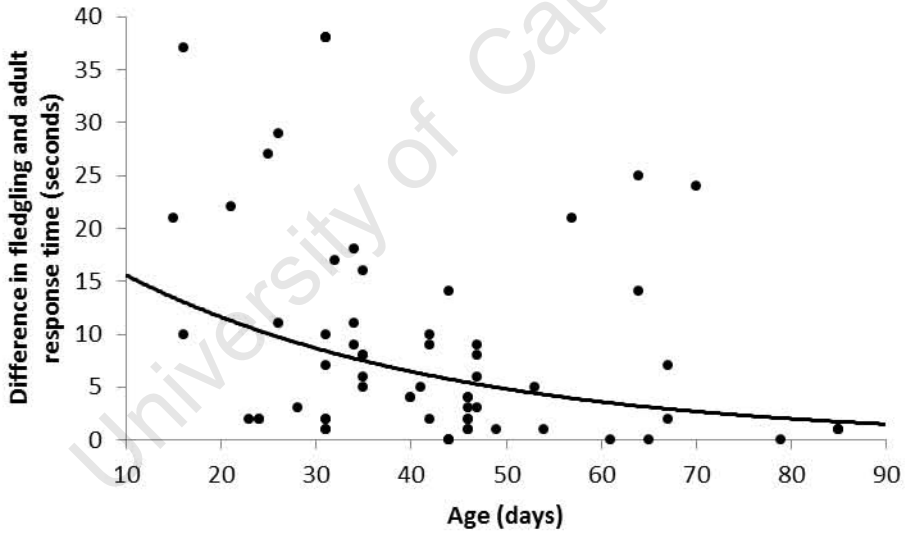

Figure 5.1 The relationship between age and response time to alarm calls. Response is defined as the time it takes a bird to reach cover after the start of the playback. The line shows the predictions from the best model investigating the difference in response time between fledglings and adults to alarm calls (Table S5.1). N=68

Table 5.1 Model selection on a series of LMM models investigating factors affecting the difference in response times between adults and fledglings to alarm calls, using information theoretic approach AICc based model selection. The response term was the $\log_{10}$ of the difference in response time between adults and fledglings, the random term was individual identity. The table lists the top 5 (with the lowest AICc values) candidate models tested. The basic model included the constant, the random terms and residual variance (σ^2). Abbreviations: Fage = fledgling age (days); Anum = adult number; Fnum = fledgling number; dCov = distance to cover (m) ratio). The models with ΔAICc <5 are in bold. See Table S5.1 for full list of candidate models. N=68

Explanatory terms	Deviance	*K*	χ^2	AICc	ΔAICc	w_i	Effect ± S.E.	
Fledgling age (days) + adult number	**-40.53**	**4**	**25.65**	**-35.9**	**0**	**0.69**	**Fage:**	**-0.013 ± 0.003**
			10.57				**Anum:**	**0.167 ± 0.051**
Fledgling age (days)	**-37.04**	**3**	**22.47**	**-32.67**	**3.23**	**0.14**		**-0.013 ± 0.003**
Fledgling age (days) + adult number + Fledgling number	**-36.07**	**5**	**26.21**	**-31.1**	**4.79**	**0.06**	**Fage:**	**-0.013 ± 0.003**
			9.99				**Anum:**	**0.200 ± 0.063**
			0.79				**Fnum**	**-0.064 ± 0.073**
Basic	-34.23	2		-30.05	5.85	0.04		
Fledgling age (days) + Adult number + Distance to cover (m)	-33.51	5	24.66	-28.54	7.35	0.02	Fage:	-0.013 ± 0.003
			10.7				Anum:	0.170 ± 0.052
			0.7				dCov:	0.018 ± 0.021

5.4.2 *Where is the most profitable location for fledglings?*

5.4.2.1 *Where do fledglings get provisioned the most?*

The most significant factors that affected provisioning rates to fledglings were location and age. Fledglings were fed at a higher rate on the ground than in trees (mean provisioning rates: ground 0.12 $g.min^{-1}$ (± 0.008 S.E.), tree 0.03 $g.min^{-1}$ (± 0.002 S.E.) (Table 5.2; LMM effect ground: 0.000 ± 0.000; tree -0.139 ± 0.013, χ^2 = 116.2). In general, provisioning rate decreased as fledglings became older (see electronic supplementary material table S5; LMM effect -0.004 ± 0.001, χ^2 = 44.19; Figure. 5.2). For a list of all candidate models tested see Chapter 5 Appendix Table S5.2.

5.4.2.2 *The effect of hunger on fledgling location*

Fledgling hunger affected their location, with supplementally fed fledglings spending more time in trees (proportion of time in trees prior to supplementation: 39.9% ± 3.1% S.E., after supplementation: 61.7% ± 4.4% S.E., paired *t*-test, t = -4.77, *d.f.* = 37, *P* < 0.001; Figure 5.3). There was no significant difference in the proportion of time that control fledglings spent in

the cover of trees between the before (41.7% ± 6.7% in trees S.E.) and after focals (46.0% ± 5.3% in trees S.E., paired *t*-test, t = -0.60, *d.f.* = 17, *P* = 0.548; Figure 5.3).

Table 5.2 Model selection on a series of LMM models investigating factors affecting provisioning rate, using information theoretic approach AICc based model selection. The response term was the square root of provisioning rate ($g.min^{-1}$), the random terms were individual and group identity. The table lists the top 5 (with the lowest AICc values) candidate models tested. Abbreviations: Fage = fledgling age (days); gr = ground; tr = tree; ADFL = adult:fledgling ratio. The models with ΔAICc <5 are in bold. See Table S5.2 for full list of candidate models. N=472

Explanatory terms	**Deviance**	***K***	**χ^2**	**AICc**	**ΔAICc**	***w_i***	**Effect ± S.E.**	
Location + Fledgling age (days)	**-1324.58**	**6**	**116.2**	**-1318**	**0**	**0.939**	**gr:**	0.000 ± 0.000
							tr:	-0.139 ± 0.013
			44.19				**Fage:**	-0.004 ± 0.001
Location + Fledgling age (days) + adult number	-1318.35	7	116.14	-1312	6.29	0.04	gr:	0.000 ± 0.000
							tr:	-0.139 ± 0.013
			42.79				Fage:	-0.004 ± 0.001
			4.51				ad:	0.010 ± 0.005
Location + Fledgling age (days) + Fledgling number	-1315.58	7	116.2	-1309	9.06	0.01	gr:	0.000 ± 0.000
							tr:	-0.139 ± 0.013
			43.84				Fage:	-0.004 ± 0.001
			0.11				fl:	0.003 ± 0.010
Location + Fledgling age (days) +adult:fledgling ratio	-1314.79	7	116.45	-1309	9.85	0.007	gr:	0.000 ± 0.000
							tr:	-0.139 ± 0.013
			43.69				Fage:	-0.004 ± 0.001
			0.62				ADFL:	0.004 ± 0.006
Location*Fledgling age (days)	-1313.13	6	2.21	-1307	11.45	0.003	gr*Fage:	0.000 ± 0.000
							tr*Fage:	-0.002 ± 0.001

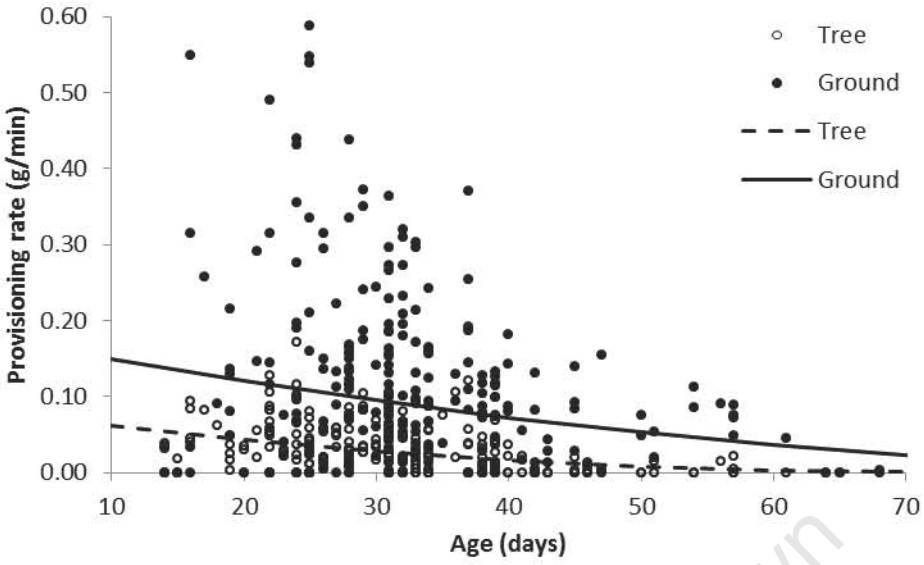

Figure 5.2 The effect of location on the relationship between age and provisioning rate (g.min^{-1}) to fledglings. Lines show the predictions from the best model for provisioning rates on the ground and in the trees related to age (Table S5). Solid line is the ground and the dashed line is for tree. N=472

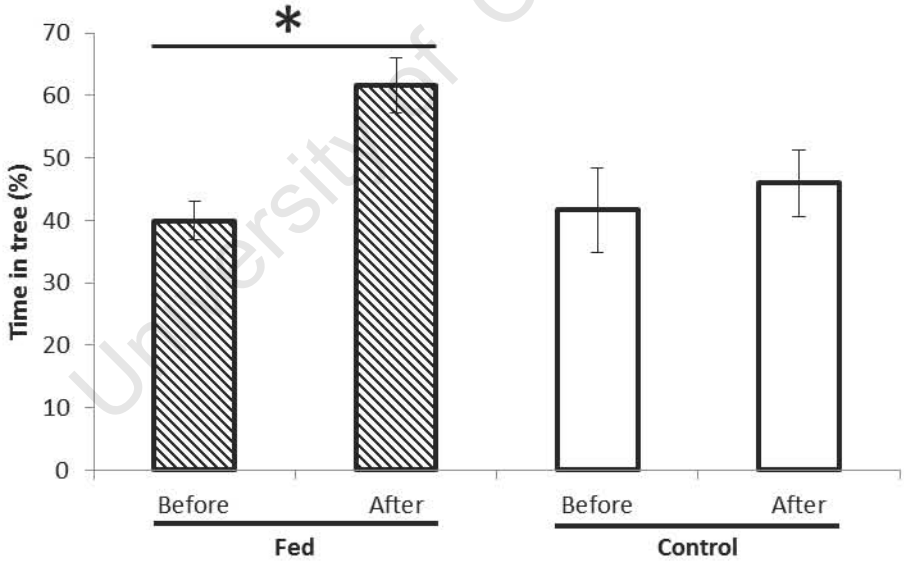

Figure 5.3 The effect of hunger on fledgling location. The effect of feeding experiment (feeding fledglings 10 meal worms) and the control on the percentage of time that fledglings spend in trees (means ± S.E.).

5.4.3 *Responses to predation risk – heterospecific alarm calls*

Control playbacks did not affect fledgling location (time on the ground (%)), terrestrial provisioning rate (g.min^{-1}) to fledglings, arboreal provisioning rate (g.min^{-1}) to fledglings or

the percentage of time that adults spent giving lead calls to fledglings on the ground (Table 5.3; Fig 5.4a-d). During playback of heterospecific alarm calls, no difference was found in the arboreal provisioning rate (g.min^{-1}) to fledglings (Table 5.3; Fig 5.4c). However, I did find a difference in location: fledglings spent less time on the ground (Fig 5.4a). In addition, following alarm call playbacks, adults provisioned terrestrially located fledglings at a higher rate and invested more time in lead calling to terrestrially located fledglings (For all means ± S.E. and p-values, see Table 5.3; Fig 5.4b & d). There was no difference in dominant and subordinate adults provisioning responses to either the control (paired *t*-test, t = -1.95, *d.f.* = 22, *P* = 0.064) or experimental (paired *t*-test, t = -1.43, *d.f.* = 22, *P* = 0.112) playbacks (see Chapter 5 Appendix Table S5.5 for means and standard errors).

Table 5.3 Results from paired analyses investigating the effects of increasing perceived predation risk. The table gives the means and standard errors for the behaviours investigated: time that fledglings spent on the ground (%); terrestrial provisioning rate (g.min^{-1}) to fledglings; arboreal provisioning rate (g.min^{-1}) to fledglings; and time that adults spent giving lead calls to terrestrial fledglings (%). Two treatments: control, with heterospecific contact calls; experimental, with heterospecific alarm calls. All paired analyses were conducted using paired *t*-tests, except for those labelled with * which were conducted using Wilcoxon Matched-pairs tests. All significant results (p<0.05) are in bold. N=24 pairs.

	Control			Experimental		
Variables	**Before**	**During**	**p-value**	**Before**	**During**	**p-value**
Time on ground (%)	33.59 ± 4.73	41.98 ± 4.82	0.286	**44.90 ± 4.26**	**27.51 ± 3.12**	**<0.001**
Terrestrial prov. (g.min^{-1})	0.13 ± 0.02	0.12 ± 0.02	0.378	**0.14 ± 0.02**	**0.27 ± 0.06**	**0.002***
Arboreal prov. (g.min^{-1})	0.017 ± 0.003	0.025 ± 0.007	0.869*	0.022 ± 0.007	0.030 ± 0.009	0.564*
Lead calls (s)	3.03 ± 0.78	1.76 ± 0.47	0.120	**1.98 ± 0.30**	**7.07 ± 1.06**	**<0.001**

5.4.4 *Causes of variation in fledgling location*

Overall, fledglings spent more time in the cover of trees than on the ground (tree: 76.64 ± 1.34% S.E.; ground: 23.34 ± 1.34% S.E.). However, this difference in location was strongly affected by fledgling age: young fledglings primarily spent their time in the cover of trees, whereas older fledglings moved to the ground more often to beg from terrestrially foraging adults (Table 5.4; LMM effect 0.022 ± 0.001, χ^2 = 374.27; Figure 5.5). In addition, fledglings in groups with fewer adults spent more time on the ground than those with more adults (Table 5.4; LMM effect -0.039 ± 0.009, χ^2 = 19.84). The total terrestrial and arboreal provisioning rates that fledglings received were all highly negatively correlated with

fledgling age and positively correlated with number of adults in the group. For a list of all candidate models tested see Chapter 5 Appendix Table S5.3.

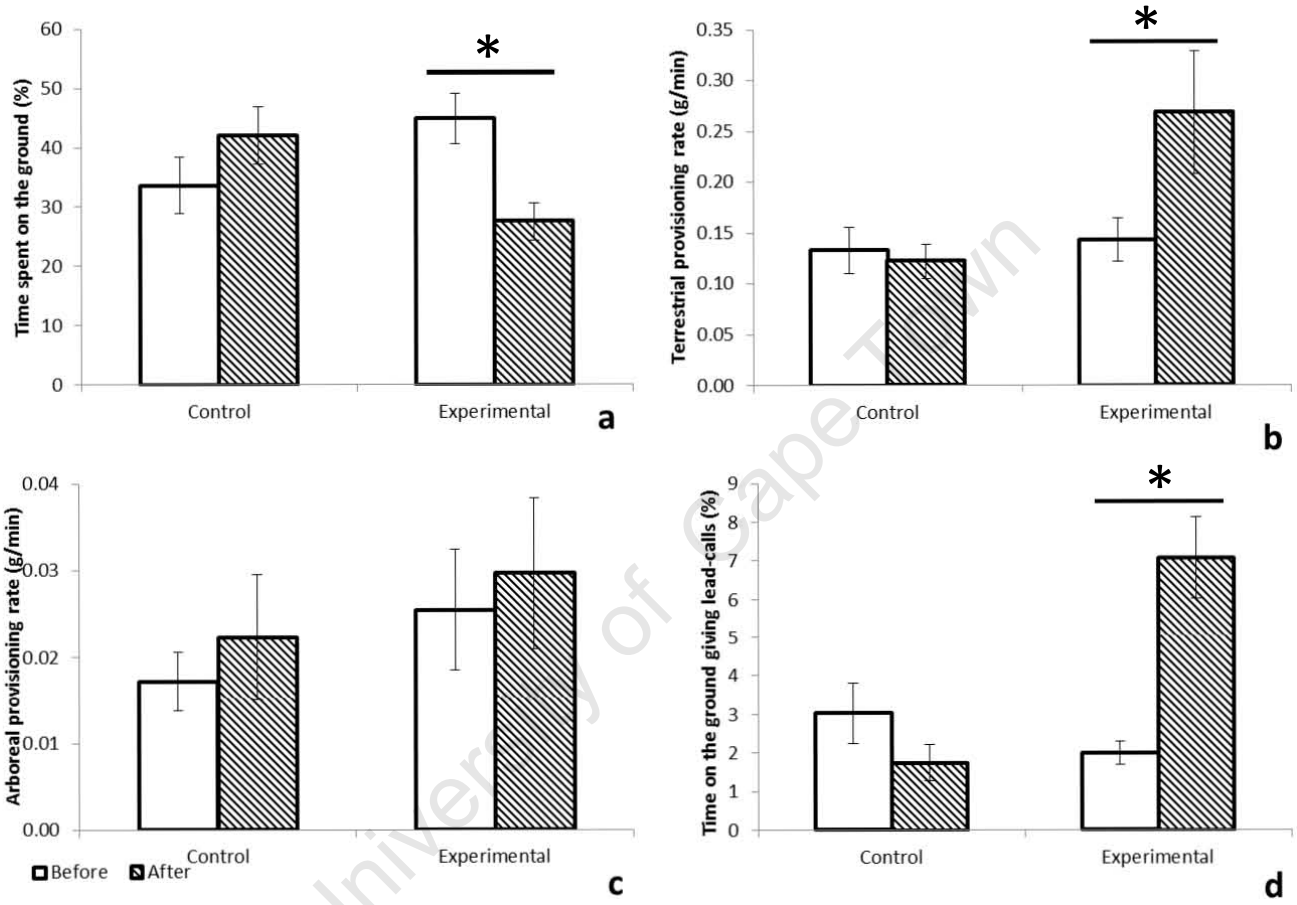

Figure 5.4 The effect of increasing percieved predation risk on **a)** time that fledglings spent terrestrially **b)** terrestrial provisioning rate ($g.min^{-1}$) to fledglings **c)** arboreal provisioning rate ($g.min^{-1}$) to fledglings **d)** percentage of time that adults give lead calls to terrestrial fledglings. All graphs plot means and standard error.

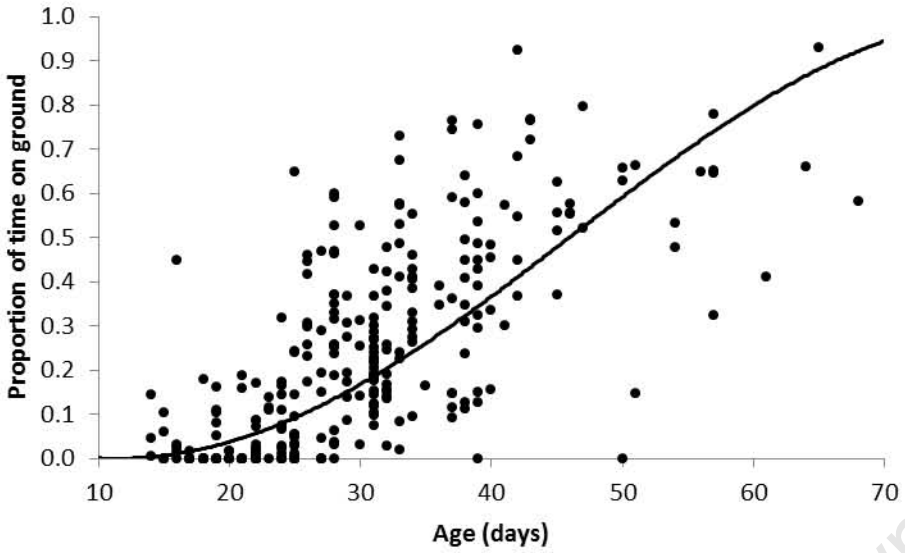

Figure 5.5 Relationship between fledgling age and fledgling location. Line shows the prediction from the best model investigating proportion of time that fledglings spend on the ground (Table S6). N=309

Table 5.4 Model selection on a series of LMM models investigating factors affecting the proportion of observation time that fledglings spend on the ground, using information theoretic approach AICc based model selection. The response term was the arcsine-square-root of the proportion of time that fledglings spend on the ground, the random terms were individual and group identity. The table lists the top 5 (with the lowest AICc values) candidate models tested. Abbreviations: Fage = fledgling age (days); Anum = adult number; Fnum = fledgling number; ADFL = adult:fledgling ratio. The models with ΔAICc <5 are in bold. See Table S5.3 for full list of candidate models. N=307

Explanatory terms	Deviance	*K*	χ^2	AICc	ΔAICc	w_i	Effect ± S.E	
Fledgling age (days) + adult number	**-609.78**	**5**	**374.27**	**-603.58**	**0.00**	**0.96**	**Fage:**	0.022 ± 0.001
			19.84				**Anum:**	-0.039 ± 0.009
Fledgling age (days) + adult number + fledgling number	-603.65	6	334.12	-597.37	6.21	0.04	Fage:	0.023 ± 0.001
			18.54				Anum:	-0.038 ± 0.009
			2.06				Fnum:	0.024 ± 0.017
Fledgling age (days) + adult:fledgling ratio	-602.67	5	361.45	-596.47	7.12	0.01	Fage:	0.024 ± 0.001
			11.17				ADFL:	-0.030 ± 0.009
Fledgling age (days)	-601.44	4	346.92	-595.31	8.27	0.02		0.024 ± 0.001
Fledgling age (days) + fledgling number	-596.12	5	351.51	-589.92	13.66	0.00	Fage:	0.024 ± 0.001
			2.75				Fnum:	0.030 ± 0.018

5.5 Discussion

In this study, I demonstrated that (a) due to slow response to alarm calls, young fledglings took longer to reach safety when on the ground than adults or older fledglings; (b) fledglings received higher feeding rates from adults when on the ground than when in the cover of

trees; and (c) adults responded to higher perceived terrestrial predation risk by elevating their provisioning rates and investing more time in leading terrestrially located fledglings back to cover. As fledglings aged, they spent longer on the ground. This is likely due to them responding faster to alarm calls and hence being at lower risk to predators. Combined, these results are consistent with Zahavi's (1977b) idea that, by increasing the risk of their own mortality, babbler fledglings can 'blackmail' adults into provisioning them at higher rates. Therefore by moving to riskier locations when hungry, fledglings may exert a greater influence on adult provisioning rate.

There are several possible alternative explanations for adults provisioning terrestrial fledglings at higher rates: i) fledglings on the ground are closer and therefore less costly to provision; ii) hungrier fledglings approach adults, who happen to be on the ground, to solicit care and fledgling location is linked to adult location; iii) terrestrially located fledglings beg more thus eliciting higher provisioning rates and; iv) movement to the ground by fledglings signals offspring quality (ability to evade predators). All hypotheses are plausible. For example, previous research has found that adults typically provision the closest offspring (Brotherton et al. 2001; Thompson & Ridley 2013), and in many species, including pied babblers (Chapter 4), hungrier offspring beg more (reviewed in Mock et al. (2011)), and I have shown that less satiated fledglings spend more time on the ground. However, the experimental evidence indicates that these are unlikely explanations for the difference in adult provisioning behaviour in relation to fledgling location. If provisioning was solely influenced by proximity, increases in predation risk should have had a uniform effect on provisioning rates. If the increased amount of time fledglings spent in the trees was solely driven by a response to predation risk, adults would not be predicted to alter their provisioning or lead calling behaviour, only fledgling location should change. If provisioning was solely related to fledgling begging levels, then again no change in provisioning rates would be predicted for increases in predation risk. Finally, if moving to the ground was a signal of quality adults would not need to alter their behaviour in relation to predation risk, as only fledglings of high enough quality would risk coming to ground. However, following experimental exposure to heterospecific alarms, arboreal provisioning rate remained

constant whilst care-givers significantly increased the provisioning and lead calling rates to terrestrially located fledglings. In addition, as fledgling mobility and response to alarm calls improved with age, analogous to being of higher quality, their ability to use moving to the ground as a signal reduces. Hence, these results show that adult provisioning behaviour is only sensitive to changes in perceived predation risk with respect to terrestrially located fledglings. Therefore, my findings support Lummaa et al.'s (Lummaa et al. 1998) hypotheses: that solicitation displays are more effective at increasing adult provisioning in predator-rich environments.

In this study I showed a novel way that fledglings can influence the amount of provisioning they received: fledglings can extract more food from adult care-givers by moving to riskier locations. Different locations (terrestrial and arboreal) have differing predation risk (Lima & Dill 1990), and the mobility of fledglings enables them to use these differences to influence adult provisioning. However, this finding poses one obvious question: why should offspring place themselves at risk? This is particularly relevant since offspring face a permanent cost, death, whereas care-givers face a smaller cost in terms of lost reproductive success or inclusive fitness (Ydenberg & Dill 1986; Redondo & Carranza 1989; Wiklund 1990). Hunger has been shown to be a major factor influencing risk tolerance in other species (Ydenberg & Dill 1986; Lima 1988). Babbler fledglings seem to show flexibility in their risk-taking, moving to riskier locations when they were hungry but staying in the cover and relative safety of trees when they were satiated. Other species have also been shown to be flexible in their risk taking, for example colonies of the ant *Lasius pallitarsis* are willing to forage in high-risk food patches when the pay-offs are higher than those in low-risk patches (Nonacs & Dill 1990). Since moving to the ground is costlier in terms of predation risk than remaining in the trees, fledglings may move to a riskier location to signal their hunger to care-givers (Zahavi 1977a; Grafen 1990). In addition, the presence of terrestrially begging fledglings may also increase the predation risk to care-givers, imposing an additional incentive on adults to provision and thus silence terrestrially located fledglings.

It is likely that the reason fledgling's trade-off risk against provisioning is because of the long-term cost of foregoing additional provisioning. In species with high reproductive skew, such as pied babblers (Nelson-Flower et al. 2011), the life-time reproductive cost of not dispersing successfully and/or acquiring a dominant position can be high (Magrath & Heinsohn 2000). As in other species, the amount of care received by pied babblers during early development has long-term effects (Lindström 1999; Ridley 2007). There is intense competition between same-sex babbler siblings, (Raihani et al. 2008), and lower quality offspring are often evicted from the group by their siblings (Raihani 2008). Evicted individuals risk becoming 'floaters', which carries a significant cost: the longer an individual is a 'floater' the greater their weight loss and the more likely they are to enter a new group as a subordinate (Ridley et al. 2008). When early condition has such profound long-term impacts, natural selection should favour the evolution of offspring behaviours that gain the greatest amount of provisioning in order to maximize their growth rate. Therefore, adults will increase their provisioning rate to fledglings when they move to the ground in order to encourage them to move back to safety. Larger groups may be able to reduce this conflict as they are able to provision fledglings at higher rates, keeping fledglings closer to satiation and so reducing the benefit they gain from moving to the ground.

The trade-off fledglings face between being fed and avoiding predators is only transient. The dependent phase is dynamic, and as such in a number of species offspring's ability to respond to predation risk improves with age and experience (Ridley & Child 2009; Magrath et al. 2010). As pied babbler fledglings age, their mobility increases and their response to alarm calls improves. The costs of being on the ground therefore decrease with improved fledgling mobility. This is analogous to the 'hide-to-follow' spectrum of young deer (Grovenburg et al. 2012): as fawns age their mobility improves and they transition from 'hiders' to 'followers' in response to predator detection. Therefore, it is likely that as a result of developmental change, babbler adults no longer need to change their provisioning behaviour when fledglings move to the ground. This highlights the fact that the dynamics of offspring-care-giver interactions are constantly changing due to offspring development (Royle et al. 2002).

Being mobile changes the environment for offspring and the mobility of pied babbler fledglings enables them to utilize their location in a signalling context. These results add to investigations into the effects of mobility on offspring-caregiver communication conducted in other species (Manser & Avey 2000; Bell 2007; Kunc et al. 2007). For example, the mobile nature of meerkat (*Suricata suricatta*) pups has led to the evolution of multiple begging call types (Manser & Avey 2000; Kunc et al. 2007). Thus, it seems likely that mobility opens up new avenues for signalling systems.

This study investigates a novel aspect of 'blackmail' by offspring to achieve higher provisioning rates. These results show that the mobility of offspring, combined with differential predation risks, can be used to influence care-givers provisioning levels. Mobile offspring may therefore be better placed to win the conflict between parents and offspring over provisioning. This study also highlights the fact that parent-offspring conflict can take place across multiple developmental stages and can be mediated by more than just begging behaviour, opening up a new avenue of investigation into conflicts and their resolution in animal societies.

5.6 Chapter 5 Appendix

The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis

Candidate models tested

For tables S5.1-S5.3: Deviance = -2 log-likelihood output of each model; *K* = number of parameters tested in each model; AICc = Akaike information criterion for a small data sets; ΔAICc = the models AICc minus the minimum AICc among candidate models. For each candidate model: Basic = basic model with no predictor terms, only constant, the random terms and residual variance (σ^2); Fage = fledgling age (days post hatching); Anum = adult number (individuals >1 year old); Fnum = fledgling number; ADFL = adult:fledgling ratio; dCov = distance to cover (m); trPrv = provision rate while in tree ($g.min^{-1}$); grPrv = provisioning rate while on the ground ($g.min^{-1}$); toPrv = total provisioning rate ($g.min^{-1}$); Loc = fledgling location (ground or tree).

Table S5.1. Difference in response time to alarm calls
N=68

Explanatory terms	Deviance	*K*	AICc	ΔAICc
Fage + Anum	-40.53	4	-35.90	0.00
Fage	-37.04	3	-32.67	3.23
Fage + Anum + Fnum	-36.07	5	-31.10	4.79
Basic	-34.23	2	-30.05	5.85
Fage + Anum + dCov	-33.51	5	-28.54	7.35
Anum	-32.85	3	-28.48	7.42
Fage + Fnum	-32.64	4	-28.01	7.89
Fage + ADFL	-32.19	4	-27.56	8.34
Fage + dCov	-29.84	4	-25.21	10.69
Fnum	-29.08	3	-24.71	11.19
ADFL	-28.89	3	-24.52	11.38
Anum + Fnum	-27.9	4	-23.27	12.63
dCov	-27.28	3	-22.91	12.99
Anum + dCov	-26.01	4	-21.38	14.52
Fage + dCov + Fnum	-25.41	5	-20.44	15.45
Fage + dCov + ADFL	-25.04	5	-20.07	15.82
dCov + Fnum	-22.13	4	-17.50	18.40
dCov + ADFL	-22.02	4	-17.39	18.51
Fage + Fnum + dCov	-21.14	5	-16.17	19.72

All LMMs were fitted with a normal distributions and identity link functions, individual identity was included as a random term to account for repeated measures.

Table S5.2. Factors effecting provisioning rate
N=472

Explanatory terms	Deviance	*K*	AICc	ΔAICc
Loc + Fage	-1324.58	6	-1318.40	0.00
Loc + Fage + Anum	-1318.35	7	-1312.11	6.29
Loc + Fage + Fnum	-1315.58	7	-1309.34	9.06
Loc + Fage + ADFL	-1314.79	7	-1308.55	9.85
Loc*Fage	-1313.13	6	-1306.95	11.45
Loc*Fage + Fnum	-1304.13	7	-1297.89	20.51
Loc*Fage + ADFL	-1303.34	7	-1297.10	21.30
Loc	-1297.74	5	-1291.61	26.79
Loc*Fage + Anum + Fnum	-1297.85	8	-1291.54	26.86
Loc + Anum	-1292.7	6	-1286.52	31.88
Loc + Fage	-1289.07	6	-1282.89	35.51
Loc + ADFL	-1288.33	6	-1282.15	36.25
Loc + Anum + Fnum	-1283.97	7	-1277.73	40.67
Fage + Anum	-1225.53	5	-1219.40	99.00
Fage + Fnum	-1222.54	5	-1216.41	101.99
Fage + ADFL	-1221.64	5	-1215.51	102.89
Fage + Anum + Fnum	-1216.44	6	-1210.26	108.14
Basic	-1210.44	3	-1204.39	114.01
Anum	-1205.17	4	-1199.08	119.32
Fnum	-1201.73	4	-1195.64	122.76
ADFL	-1200.92	4	-1194.83	123.57
Anum + Fnum	-1196.39	5	-1190.26	128.14

All LMMs were fitted with a normal distributions and identity link functions, individual and group identity were included as random terms to account for repeated measures.

Table S5.3. Proportion of time fledglings spent on the ground
N=307

Explanatory terms	Deviance	*K*	AICc	ΔAICc
Fage + Anum	-609.78	5	-603.58	0.00
Fage + Anum + Fnum	-603.65	6	-597.37	6.21
Fage + ADFL	-602.67	5	-596.47	7.12
Fage	-601.44	4	-595.31	8.27
Fage + Fnum	-596.12	5	-589.92	13.66
trPrv	-432.56	4	-426.43	177.15
trPrv + ADFL	-426.2	5	-420.00	183.58
trPrv + Fnum	-425.35	5	-419.15	184.43
Anum	-398.93	4	-392.80	210.78
grPrv	-385.31	4	-379.18	224.40
Basic	-383.93	3	-377.85	225.73
toPrv	-382.72	4	-376.59	226.99
grPrv + ADFL	-380.34	5	-374.14	229.44
adfl	-378.86	4	-372.73	230.85
grPrv + Fnum	-378.74	5	-372.54	231.04
Fnum	-377.43	4	-371.30	232.28

Table S5.4: Predictor weights for all variables investigated in each candidate model set

Model	Predictor terms	Weight
a) Fledgling response to alarm calls	**Fledgling age (days)**	**0.975**
	Adult number	**0.791**
	Fledgling number	0.081
	Adult:fledgling ratio	0.013
	Distance to cover (m)	0.023
b) Provisioning rate ($g.min^{-1}$)	**Location (ground or tree)**	**1.000**
	Fledgling age (days)	**1.000**
	Adult number	0.040
	Fledgling number	0.010
	Adult:fledgling ratio	0.007
c) Proportion of time on the ground	**Fledgling age (days)**	**1.000**
	Adult number	**0.958**
	Fledgling number	0.042
	Adult:fledgling ratio	0.026
	Tree prov. rate ($g.min^{-1}$)	$3.33x10^{-39}$
	Total prov. rate ($g.min^{-1}$)	$4.69x10^{-50}$
	Ground prov. rate ($g.min^{-1}$)	$2.00x10^{-50}$

Predictor weights for the all variables investigated in LMMs. Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable (Symonds & Moussalli 2011). Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011). All variables deemed to be important are in bold.

Table S5.5: Results from paired analyses investigating the difference in provisioning behaviour

	Control			Experimental		
Variables	**Before**	**During**	**p-value**	**Before**	**During**	**p-value**
Biomass (%)	39.92 ± 8.32	52.96 ± 7.14	0.064	34.40 ± 6.84	45.17 ± 7.51	0.112
Feeds (%)	37.28 ± 8.03	47.19 ± 6.81	0.166	30.90 ± 6.34	41.11 ± 7.25	0.116

Table S9 gives the means and standard errors for the proportion of biomass fed to fledglings by dominants and the proportion of feeds to fledglings by dominant individuals. All p-values were generated by conducting using paired *t*-tests to compare feeding behaviours before and after control and experimental playbacks.

Chapter 6

Investigating the factors that affect foraging development

Investigating the factors that affect foraging development

6.1 Abstract

The acquisition of foraging skills plays a crucial role in the life-histories of many species, influencing dispersal, reproduction and survival. In species that exhibit parental care, a major part of foraging skill development occurs while offspring are still nutritionally dependent on adult care-givers. However, offspring often have limited control over their duration of care. Understanding how offspring maximize their foraging development within these constraints is important in understanding behavioural flexibility. The prolonged period of care exhibited by cooperative breeders offers an ideal opportunity to investigate the factors influencing foraging development. Using pairs of same-sex siblings and feeding experiments, I investigated three potential factors influencing foraging skill development in pied babblers: initial factors (initial ability and condition), investment in foraging and investment in offspring-adult associations. I found that initial foraging ability and condition, as well as investment in offspring-adult associations did not correlate with foraging efficiency at one year. However, individuals who invested more in foraging, promoting individual-learning, when younger had higher foraging efficiency at one year. Supporting this result, experimentally satiated fledglings invested more time in foraging than in associations with adult care-givers. The development of behaviour involves the interaction between social and individual-learning. These results suggest that, for fledgling pied babblers, investment in individual-learning behaviours is the key predictor of foraging skill at adulthood.

6.2 Introduction

The prolonged period of care exhibited by cooperative breeding species offers an ideal opportunity for offspring to develop foraging skills (Langen 1996a; Thornton & McAuliffe 2006). However, offspring have little control over the environment they are born into (Kilner & Hinde 2012) and in many situations they may have relatively little control over the care they receive (Mauck & Grubb Jr 1995; Verhulst & Hut 1996; Ghalambor & Martin 2001; Ridley & Raihani 2007a; Thorogood et al. 2011). Thus, offspring may be fixed on a developmental trajectory, or conversely they may be able to invest in alternative behaviours

to maximize their life-history prospects given the hand they have been dealt. The development of foraging skills has strong effects on life-history traits such as dispersal (Ridley & Raihani 2007a), reproduction (Heinsohn 1991; Langen 1996b) and survival (Clutton-Brock et al. 2001; Hodge et al. 2009). Therefore, learning foraging skills is a crucial part of offspring development (Heinsohn 1991; Langen 1996b). In many altricial species, offspring develop their foraging skills during the course of their dependent phase (Sullivan 1988; Yoerg 1994; Langen 1996b; Thornton 2008a). In this study, I seek to understand how three categories of factors influence an individual's foraging development: initial factors (initial foraging ability and condition), investment in foraging, and investment in offspring-adult associations.

The 'silver-spoon' hypothesis posits that food availability early in life can have long-term effects on an individual's life-history (Grafen 1988; Lindström 1999). Therefore, it is possible that individuals born with an initial advantage, e.g. in mass, will in the long-term always have better life-history outcomes than their siblings, dispersing earlier and gaining higher life-time reproductive success (Grafen 1988; Cockburn 1991). Such long-term effects of early body condition have been shown to exist in a variety of species (see Lindström 1999 for a review). Early life effects can manifest themselves in a variety of ways that influence life-history outcomes, with early condition shown to influence male reproductive success in red deer (*Cervus elaphus*) (Kruuk et al. 1999), survival and quality of territory acquired in Eurasian oystercatchers (*Haematopus ostralegus*) (Van de Pol et al. 2006), reproductive rate in mouthbrooding cichlids (*Simochromis pleurospilus*) (Taborsky 2006) and the attractiveness of male mosquito fish (*Gambusia holbrooki*) (Kahn et al. 2012). Such long-term effects of early-life are not restricted to uni- and biparental species. Hodge et al. (2009) showed that in the communally breeding banded mongoose, pups born from heavy mothers were heavier at birth, had higher competitive ability and higher survival than their smaller littermates. Meerkat pups in good condition early in life developed greater foraging efficiency after independence (Thornton 2008a). Therefore, early-life advantages have the potential to cause long-term differences in foraging ability between siblings.

Although initial condition may have lasting effects on foraging ability, there are many examples of animals improving their behaviours through experience, such as: female mate

choice (Kodric-Brown & Nicoletto 2001), courtship (Dukas 2005), begging calls (Madden & Davies 2006), behaviour in dominance interactions (Schuett 1997) and parental behaviour (Margulis et al. 2005). There is a wealth of evidence to show that foraging skills develop through individual-learning, for example via trial-and-error, as foraging skills commonly improve with experience (Brown 1987; Rovero et al. 1999; Warburton 2003; Wheelwright & Templeton 2003). The fine-tuning of an individual's foraging skills has been shown to be affected by experience in a variety of animal taxa (Flores et al. 1989; Laland & Plotkin 1992; Dukas & Visscher 1994; Mackney & Hughes 1995). Trial-and-error learning has been proposed to facilitate learning of complex skills, such as the honing of termite fishing skills in chimpanzees (*Pan troglodytes*) (Lonsdorf 2005). Learning of skills through individual experience is therefore likely to contribute to foraging skill development in many species. If individual-learning is important for the development of foraging skills, then I would expect that offspring who invested heavily in foraging when young would develop higher foraging efficiencies later in life.

In some animal species socially acquired, as well as personally acquired, information is used to inform individual decisions (Giraldeau 1984; Galef & Giraldeau 2001; Dall et al. 2005). Much laboratory and field work has been carried out to investigate how social information is transferred, either through social facilitation, local enhancement, public information or teaching (Giraldeau & Templeton 1991; Caro & Hauser 1992; Danchin et al. 2004; Thornton & McAuliffe 2006; Acerbi et al. 2007; Raihani & Ridley 2008a; Thornton & Raihani 2008). In several species, social influences have been noted to influence the development of foraging skills in other individuals (Terkel 1996; Visalberghi & Addessi 2000; Reader & Laland 2000; Addessi et al. 2005; Schiel & Huber 2006; Thornton & McAuliffe 2006; Thornton 2008b). The long periods of offspring care characterised by cooperative species (Langen 2000), provide the opportunity for offspring to learn foraging skills from other group members (Langen 1996a; Thornton & Raihani 2008). Many of these cooperative species exhibit close foraging associations between offspring and adult care-givers (e.g., Florida scrub-jays (*Aphelocoma coerulescens*) (McGowan & Woolfenden 1990), white-throated magpie-jays (*Calocitta formosa*) (Langen 1996a), meerkats (Hodge et al. 2007) and banded mongoose (Gilchrist 2004)). These associations offer the ideal opportunity for young to observe and socially learn what to eat, when to eat, where to find prey and how to eat it from experienced individuals

(Galef & Giraldeau 2001). If offspring-adult associations are used to facilitate social-learning of foraging skills, then I would expect that offspring who invested heavily in offspring-adult associations during dependence would develop higher foraging efficiencies when they became older.

In order to optimize their behaviour, individuals have to trade-off long-term and short-term benefits (Ydenberg & Dill 1986; Ghalambor & Martin 2001). Different behaviours will provide different pay-offs and may be constrained by energetic demands (Davies 1976; Thornton 2008a). For example, if an individual's foraging skills are poor then their short-term pay-offs may be low, but there is the potential for a long-term pay-off in improved foraging skills (Thornton 2008a). Conversely, associating with care-givers may yield large short-term pay-offs, in the form of higher provisioning rates (Brotherton et al. 2001; Gilchrist 2004; Thompson & Ridley 2013), but these associations may also lead to long-term pay-offs though socially acquired foraging skills (Midford et al. 2000; Thornton & Hodge 2008). An individual's energetic state may alter the optimal behaviour to invest in by altering the potential pay-offs from different behaviours (Waelti & Reyer 2007). By reducing an individual's short-term energetic constraints, it may reduce the need to invest in behaviours with short-term provisioning benefits and allow them to perform behaviours that maximizes long-term pay-offs.

In this chapter, I investigate which factors are most important in foraging skill development in fledgling pied babblers. These cooperatively breeding passerines have a prolonged period of post-fledging care where all group members provision fledglings (Raihani & Ridley 2007b; Ridley & Raihani 2007a; Raihani & Ridley 2008a). Once offspring fledge and become mobile, they form temporary dyadic associations with foraging adults, where they follow and beg for food from a specific adult for a short period of time, before switching to a different care-giver (Thompson & Ridley 2013). In pied babblers, it is already known that longer periods of post-fledging care result in improved adult foraging efficiencies, greater body mass and earlier dispersal (Ridley & Raihani 2007a). However, it is not known whether fledgling foraging efficiency at nutritional independence is affected by initial factors, such as condition at the time of fledging or initial foraging ability. I also test whether fledglings maximize their

foraging skill development either through increasing their investment in foraging or associating with adult care-givers.

I followed pairs of same-sex siblings through their foraging development to determine the relative importance of initial factors, foraging and offspring-adult associations during early life on the development of foraging skills in fledgling pied babblers. This enabled me to control for confounding factors and to determine if initial differences persisted or if investment in certain behaviours influenced foraging skill development. Additionally, I carried out a supplemental feeding experiment to investigate which behaviours fledglings preferentially invested in when their short-term energetic constraints were relaxed. I predicted that fledglings would increase their investment in behaviours that maximized their foraging skill development when energetic constraints were reduced.

6.3 Methods

6.3.1 *Study site and species*

Research was conducted at the Pied Babbler Project, based at the Kuruman River Reserve, South Africa. The foraging behaviour of pied babblers consists of the excavation of buried prey or the gleaning of prey from the surface of the substrate (Child et al. 2012). Pied babblers catch a wide variety of prey, varying from larval and adult stage insects to arachnids and small lizards (Child et al. 2012). During the prolonged post-fledgling dependent phase of pied babblers, offspring are mobile and move freely within the group, soliciting care from individual adults during short-term dyadic associations (as described above) (Thompson & Ridley 2013). For the sake of clarity in this chapter, I will refer to these as 'associations', but Thompson & Ridley (2013) referred to this behaviour as 'social-foraging'. Associations were defined as when a fledgling was less than 50 cm from a foraging adult, and was begging from and following that adult for more than 5 s (Thompson & Ridley 2013). Associations can range in duration from 5 to 595 s (mean: 45.6 s ± 1.3 s S.E.). When a fledgling is associating with a care-giver it can also engage in its own foraging behaviour. Pied babblers are predominantly terrestrial foragers, with more than 95% of adult foraging and all associations occurring on the ground (Ridley & Raihani 2007b; Thompson & Ridley 2013). See Chapter 2 for further details about the study site and population, and the natural history of pied babblers.

6.3.2 *Data collection*

Detailed 20-minute focal observations ('focals') (Altmann 1974) were conducted on individuals between the ages of 20 and 365 days post-hatching. Birds were followed at a distance of between 2 and 5 m and the time they spent performing all behaviours was recorded (s). Behaviours recorded were: time spent foraging (s); items caught while foraging (g); time spent on the ground or in trees (s); and the time spent associating (s) (see Thompson & Ridley (2013) for description). While on the ground and in trees, fledglings can engage in other behaviours, such as preening, play fighting or resting. These other behaviours were not included in these analyses. Food item sizes and weights were calculated using the methods detailed in Chapter 2, and the same as Ridley & Raihani (2007a). All focal observations were conducted in the morning, once the group had started foraging, between 0700 and 0930. Focal observations were not conducted during inter-group-interactions or major predator events, and all observations were aborted upon the start of one of these events. All focal observations were paused when the bird was out of sight and resumed when the bird was back in clear view. If the break in observation time was longer than 5 minutes the focal was terminated. If the bird was engaged in an activity (e.g. foraging) at the end of the 20-minute focal observation, the observation was not terminated until it changed activity (Thornton 2008a). Due to these disturbances, focal length varied and average focal length was 19 min 31 s (± 5.4 sec S.E.). All behavioural data collection was carried out using a hand held computer (Palm T|X, Palm Inc™). An individual's foraging skill was assessed by calculating its foraging efficiency (biomass caught (g) per minute of foraging). Time spent foraging and associating (s) were both calculated as a proportion of the length of the focal observation period. To investigate how current food abundance affected foraging efficiency, I used the total amount of rainfall (mm) in the 60 days preceding the focal observation, as insect abundance has been shown to lag behind rainfall (Cumming & Bernard 1997). To determine if environmental conditions prior to hatching and fledging influenced an individual's foraging skills I used the total amount of rainfall (mm) in the 60 days preceding hatching and fledgling. For details on rainfall data collection see Chapter 2. Generalized linear mixed models (GLMMs) were then used to investigate the factors affecting foraging efficiency, using data from 644 focal observations on 102 fledglings from 16 groups.

Just prior to fledging (11 days post-hatching), all chicks were weighed to the nearest 0.5 g and had their tarsi measured to the nearest 0.1 mm. Body condition was estimated as the residual of a regression of nestling mass (g) on tarsus length (mm). I will henceforth refer to this residual as nestling condition. Nestling condition gives a measure of energy storage relative to skeletal size (Jakob et al. 1996). Post-fledging body mass at one year was measured by using a small (<0.5 g) food reward (cooked crumbed egg yolk) to entice individuals onto a top-balance scale (Ridley et al. 2008), see Chapter 2 for further details. All weights were collected using an Ohaus Scout Pro II SPU2001 (Ohaus Corp.™). It was not possible to get measures of offspring condition after chicks had fledged, as this would have required trapping fledglings. Trapping has negative effects on the habituation of birds, affecting all areas of data collection. In addition, pied babblers do not regularly get onto the scale until fairly late in their dependence, making the collection of young fledgling weights difficult.

6.3.3 *The effect of associations on provisioning and foraging*

To determine what short-term benefits fledglings gained from associations, I investigated the influence of associations on provisioning rates to fledglings and fledgling foraging efficiency. I used focal observation data collected on fledglings between 20 and 100 days post-hatching. In addition to the behaviours mentioned above, the prey type and size of all items fed to fledglings during focal observations were recorded. Again, all food item sizes and weights were calculated using the methods described in Chapter 2. All provisioning events and foraging bouts were classified as either 'association' or 'alone'. Provisioning rates ($g.min^{-1}$) were calculated as biomass fed per minute of being 'alone' or 'associating'. Similarly, foraging efficiencies ($g.min^{-1}$) were calculated as biomass caught per minute of foraging 'alone' or foraging while 'associating'. In addition, the proportion of foraging that was carried out while associating was also calculated. All focals where fledglings did not form any associations with care-givers were excluded from all analyses. Focals where fledglings did not forage were excluded from the foraging analysis. Data were split into four evenly spaced age categories: 20-39, 40-59, 60-79 and 80-100 days post-hatching. Paired *t*-tests were conducted on within focal data, to determine if provisioning rates and foraging efficiency were higher while fledglings were associating within the different age categories.

6.3.4 *Factors affecting adult foraging ability*

To investigate the factors that influenced foraging skill development, I conducted paired analyses using same-sex siblings from the same brood (12 pairs of chicks followed to 120 days and eight pairs followed to one year). The data used for analysis were from multiple focal observations (3-5 per fledgling) conducted within a week of fledglings being at each age of interest: 50, 120 and 365 days post-hatching. Fifty days represents the peak period of begging and association behaviour (Chapter 3). Thus, 50 days was chosen as the age to represent initial fledgling foraging ability (foraging efficiency) and investment in foraging and associating, as it is at the lower limit at which some fledglings cease to be cared for by adults (Ridley & Raihani 2007a). At 120 days, the majority of fledglings have ceased begging (Chapter 3) and are therefore likely to be nutritionally independent. Hence, fledgling foraging efficiency at 120 days is likely to have important life-history implications. Pied babblers are able to disperse at one year (Raihani et al. 2010), and previous research has shown that foraging ability at this age affects dispersal ability (Ridley & Raihani 2007a), thus I chose one year to represent adult levels of foraging.

By pairing siblings I was able to control for many external factors (environment, group size, territory and sex), enabling me to determine if investment in different behaviours or initial factors influenced development. I investigated three categories of potential factors: 1. Initial factors (nestling condition and foraging ability at 50 days post-hatching); 2. Investment in foraging; and 3. Investment in associations. The proportion of time spent foraging is likely to give a good indication of the importance of individual-learning, as this activity provides the opportunity for trial-and-error learning (Thornton 2008a). The close proximity of fledglings in associations with foraging adults care-givers provides offspring with the opportunity for social-learning (Thornton & Hodge 2008). As such, the effect that fledgling investment in associations has on foraging development can be used to indicate if associations are used for the social-learning of foraging skills. For pairs of same-sex siblings from the same brood, initial foraging efficiency and levels of foraging and association were calculated from focal observations (detailed above) carried out on fledglings at 50 days post-hatching. Based on these values, I classified each member of the pair as either high or low in: initial foraging ability (50 days); nestling condition; time spent foraging (50 days); and time spent associating (50 days). These factors were then tested for correlation and were found to all be

independent of each other. Paired *t*-tests were conducted to investigate whether fledglings with relatively higher initial levels of foraging ability, nestling condition, foraging or association developed higher foraging efficiency ($g.min^{-1}$) at 120 days and one year.

6.3.5 *Influence of satiation on behaviour*

To investigate which behaviours fledglings preferentially invested in during periods of relaxation in their energetic constraints, I carried out a supplemental feeding experiment to influence short-term energy budgets. Fledglings were initially observed for 20-minutes ('before' focal), then fed a number of supplemental meal worms in one of three treatments: 1 worm, 5 worms or 10 worms. These treatments represent a range of satiation levels (Chapters 3 & 5), and hence a range in the relaxation of energetic constraints. A second 20-minute focal ('after' focal) was then carried out. I investigated whether fledglings preferentially invested time in foraging or associations, as these behaviours have the potential to promote individual-learning (foraging) and social-learning (association). The proportion of time invested in these behaviours was corrected for the amount of time that fledglings spent on the ground, because satiated fledglings spent longer in the safety of trees than unsatiated fledglings (Chapter 5). Supplemental feeding experiments were conducted on 48 fledglings from 13 different groups. GLMMs were used to assess the importance of factors affecting investment in foraging and association.

6.3.6 *Statistical analyses*

Analyses were conducted using R (v. 2.15.0). I used paired *t*-tests to investigate the influence of association on provisioning rates and foraging efficiency, as well as the influence of initial factors, foraging and association on foraging skill development. GLMMs with normal distributions and identity link functions created using the package lme4 (v. 0.999375-42), were used to determine the variables most important in influencing (i) foraging efficiency (ii) proportion of time on the ground that was spent foraging (iii) proportion of time on the ground that was spent associating. I adopted an information-theoretic approach using Akaike's information criterion (AIC) (Burnham & Anderson 2002; Burnham et al. 2011). Hurvich and Tsai's correction of Akaike's information criterion for small sample size (AICc) (Hurvich & Tsai 1989) was used for model selection investigating models with small sample sizes (where n/k <40), models ii and iii (Anderson et al. 2000). The effects of fixed terms

were considered using maximum-likelihood estimation. Group and individual identity were used as random terms to account for the effect of repeated measures. The other potential explanatory factors investigated in the models were fledgling age (days post-hatching), fledgling sex (male or female), group size (number of adults), brood size (number of fledglings), adult:fledgling ratio, rainfall before the focal observation (mm), rainfall before hatching (mm) and rainfall before fledging (mm). To take into account the paired nature of the feeding experiment, an additional factor was included in the analysis of experimental results: the interaction between focal observation type ('before' or 'after' treatment) and treatment (number of worms fed). I created a set of *a priori* candidate models, each with the basic model and a number of non-correlated explanatory terms. Linear regression was used to check for collinearity in all explanatory terms: correlated terms were never included in the same model. Models were then ranked in order of their AIC or AICc values, with models with lower AIC or AICc values being those with greatest explanatory power. Overall, the model with the highest Akaike weight (w_i) and lowest AIC or AICc value was considered the best. Models with ΔAIC or ΔAICc <5 were considered to have at least some support (Burnham & Anderson 2002), and when more than one model had some such support, the importance of explanatory terms was evaluated by calculating the predictor weight for each term using the method described in Symonds & Moussalli (2011). The residuals from all models were checked for normality. Prior to creating models, tests for normality were conducted on all data; if data were non-normally distributed they were transformed. Proportional data were arcsine-square-root or square-root transformed to achieve normality.

6.4 Results

6.4.1 *Development of foraging efficiency*

Multiple models obtained similar levels of support (ΔAIC <5: see Table 6.1 & S6.1), so I used predictor weights to determine the most important variables (see Chapter 6 Appendix Table S6.4). Given the data, the most important factors predicting foraging efficiency were age, age^2, rainfall before the focal observation and rainfall before hatching. Age is an important determinant of foraging ability and for this data set its effect was quadratic (age: GLMM effect 0.004 ± 0.0003, χ^2 = 452.99; age^2: GLMM effect -6.5x10^{-6} ± 6.5x10^{-7}, χ^2 = 78.71: Figure. 6.1). The amount of rainfall before the focal observation was carried out was also important (GLMM effect 0.0008 ± 0.0001, χ^2 = 42.87), as well as the amount of rainfall before the

individual hatched (GLMM effect -0.0004 ± 0.0001, χ^2 = 22.87). For a list of all candidate models tested see Chapter 6 Appendix Table S6.1. Early foraging success was very poor, with many fledglings failing to catch any prey during focal observations, explaining the shape of the predicted line in Figure 6.1 at low fledgling ages.

6.4.2 *The effect of associations on provisioning and foraging*

Pied babbler fledglings forage while alone and while associating with adult care-givers (Figure 6.2a). Associations appear to benefit fledglings in two ways. First, when fledglings were young, between 40-59 days post-hatching, their foraging efficiency was higher while associating than while foraging alone (Figure 6.2a; Table 6.2). Secondly, when fledglings were younger than 80 days post-hatching, they were provisioned at higher rates when they were in associations than when they were not (Figure 6.2b; Table 6.2).

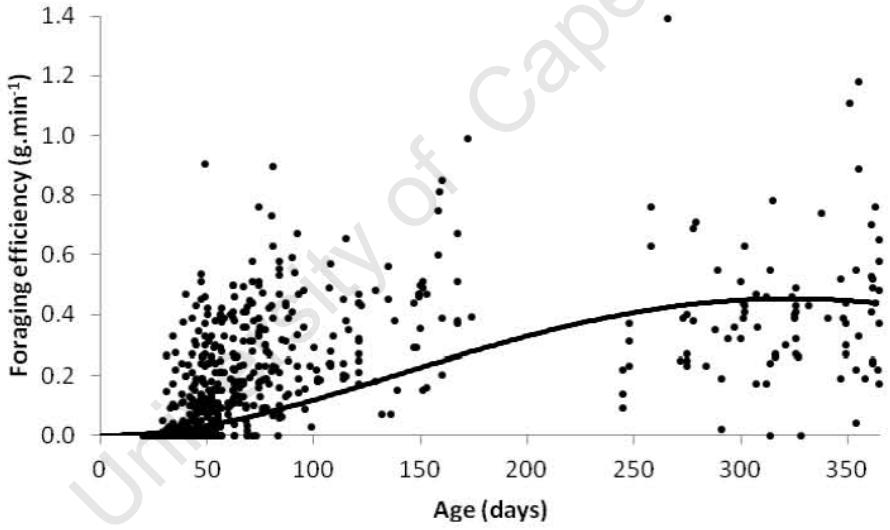

Figure 6.1 The relationship between age and foraging efficiency (g.min^{-1}) for 644 20-min focal observation periods of pied babbler juveniles of known age. The line shows the predictions from the best model investigating the factors affecting the fledgling foraging efficiency (see Table 6.1.).

6.4.3 *Factors influencing foraging efficiency*

None of the factors investigated had a significant effect on individual foraging efficiency at 120 days. Fledglings with higher foraging efficiency (paired *t*-test, t = 0.03, *d.f.* = 11, *P* = 0.973), who spent longer foraging (paired *t*-test, t = -0.75, *d.f.* = 11, *P* = 0.466) or who spent longer associating at 50 days post-hatching (paired *t*-test, t = 1.55, *d.f.* = 11, *P* = 0.143) did not have significantly different foraging efficiency at 120 days.

Table 6.1 Model selection on a series of GLMM models investigating factors affecting fledgling foraging efficiency ($g.min^{-1}$). The response term was the square-root of foraging efficiency ($g.min^{-1}$). Abbreviations; Fage = fledgling age (days); $Fage^2$ = fledgling age^2; Fsex = fledgling sex (female or male); Anum = number of adults in the group; Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio; brood = brood number; rnfl.b4.htch = cumulative rainfall for the two months preceding hatching; rnfl.b4.fl = cumulative rainfall for two months prior to the fledging; rnfl.b4.fcl = cumulative rainfall for two months prior to the focal. All GLMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. All models with ΔAIC <2 are in presented. N = 644.

Explanatory terms	Deviance	*K*	AIC	ΔAIC	w_i	Effects ± S.E.	
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before hatching + Fledgling number + Brood number	-277	10	-257.0	0.0	0.16	Fage:	0.004 ± 0.0003
						Fage²:	$-6.5x10^{-6} \pm 6.8x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.htch:	-0.0004 ± 0.0001
						Fnum:	0.020 ± 0.012
						brood 1:	0.000 ± 0.000
						brood 2:	-0.034 ± 0.021
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before hatching + Fledgling number	-274.8	8	-256.8	0.2	0.15	Fage:	0.004 ± 0.0003
						Fage²:	$-6.6x10^{-6} \pm 6.8x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.htch:	-0.0006 ± 0.0001
						Fnum:	0.021 ± 0.013
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before hatching + Brood number	-274.5	9	-256.5	0.5	0.13	Fage:	0.004 ± 0.0003
						Fage²:	$-6.6x10^{-6} \pm 6.9x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.htch:	-0.0004 ± 0.0001
						brood 1:	0.000 ± 0.000
						brood 2:	-0.034 ± 0.022
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before hatching + Adult:fledgling ratio	-274.2	8	-256.2	0.8	0.11	Fage:	0.004 ± 0.0003
						Fage²:	$-6.6x10^{-6} \pm 6.9x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.htch:	-0.0005 ± 0.0001
						ADFL:	-0.010 ± 0.007
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before hatching	-272	7	-256.0	1.0	0.10	Fage:	0.004 ± 0.0003
						Fage²:	$-6.6x10^{-6} \pm 6.8x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.htch:	-0.0005 ± 0.0001
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before fledgling + Fledgling number	-273.4	8	-255.4	1.6	0.07	Fage:	0.004 ± 0.0003
						Fage²:	$-6.6x10^{-6} \pm 6.8x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.fl:	-0.0004 ± 0.00005
						Fnum:	0.021 ± 0.012
Fledgling age + Fledgling age² + Rainfall before the focal + Rainfall before fledging + Adult:fledgling ratio	-273.3	8	-255.3	1.7	0.07	Fage:	0.004 ± 0.0003
						Fage²:	$-6.5x10^{-6} \pm 6.8x10^{-7}$
						rnfl.b4.fcl:	0.0008 ± 0.0001
						rnfl.b4.fl:	-0.0004 ± 0.00009
						ADFL:	-0.01 ± 0.007

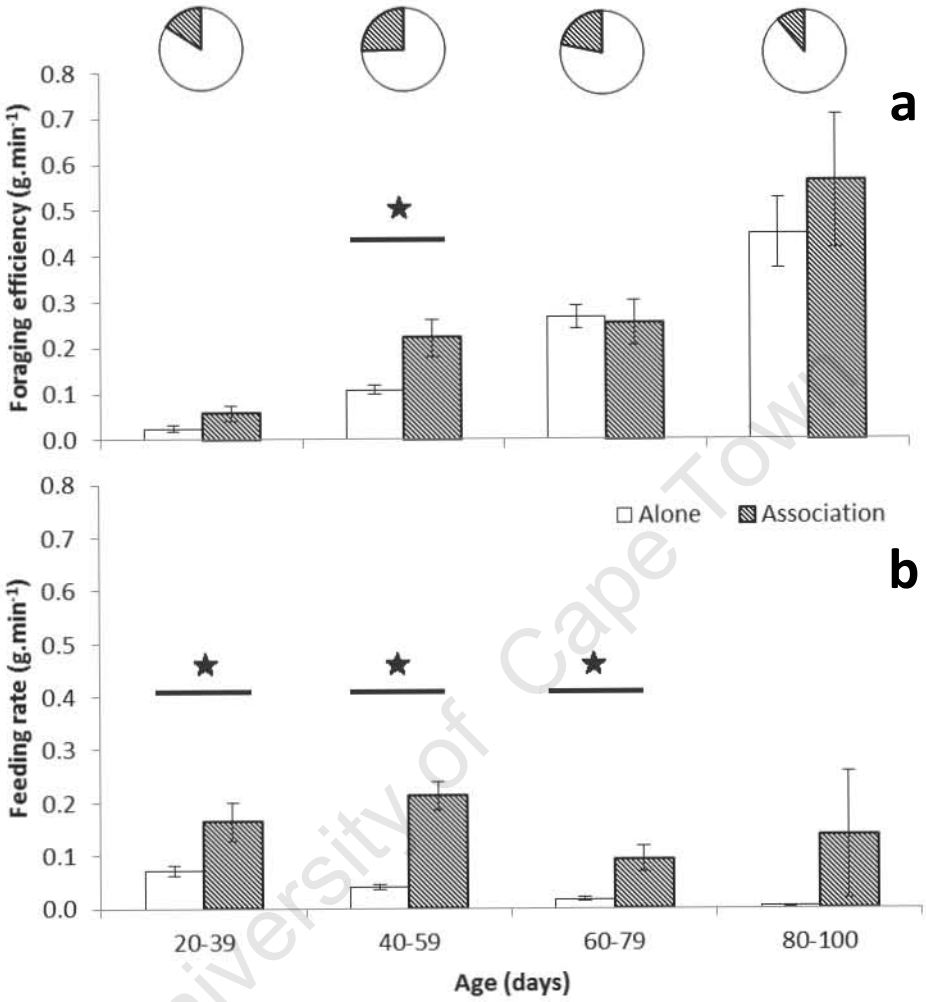

Figure 6.2a) The foraging efficiency (g.min^{-1}) of fledgling pied babblers when they were foraging alone and when they were foraging during associations, at different ages and **b)** shows the provisioning rate (g.min^{-1}) that fledglings received whilst alone or whilst in associations, at different ages. The pie charts show the proportion of foraging that occurred when fledglings were foraging alone or foraging during associations. Open bars and sections of the pie charts refer to when fledglings were alone and shaded bars and sections of the pie chart refer to when fledglings were associating. Values presented are means ± standard errors from 377 20-minute focal observations of 97 fledglings from 15 groups.

Table 6.2 Shows the *P*-values and test statistics for a series of paired *t*-tests carried out to investigate two questions. Firstly, were fledglings provisioned at higher rates while in associations or not in associations? Secondly, did fledglings have a higher foraging efficiency during associations or while foraging alone? All significant results are in bold.

Age range (days post-hatching)	Provisioning rate (g.min-1)			Foraging efficiency (g.min-1)		
	t	*d.f.*	*P*-value	t	*d.f.*	*P*-value
20-39	**-2.42**	**55**	**0.018**	-1.55	38	0.130
40-59	**-6.43**	**152**	**<0.001**	**-2.41**	**140**	**0.017**
60-79	**-3.14**	**70**	**0.002**	0.54	64	0.593
80-100	-1.12	28	0.274	-0.6	22	0.557

Fledglings who had higher foraging efficiency (paired *t*-test, t = 0.25, *d.f.* = 7, *P* = 0.806) and who spent longer associating at 50 days post-hatching (paired *t*-test, t = 0.56, *d.f.* = 7, *P* = 0.586) did not have significantly higher foraging success at one year, but individuals that invested more in foraging at 50 days had significantly higher foraging efficiency at one year, with a mean of 0.63 g.min^{-1} ± 0.09 S.E. compared to 0.39 g.min^{-1} ± 0.05 S.E. (paired *t*-test, t = 2.32, *d.f.* = 7, *P* = 0.040: Figure 6.3).

At no point during an individual's life did nestling condition have a significant effect on foraging efficiency: 50 days (paired *t*-test, t = -0.70, *d.f.* = 11, *P* = 0.496), 120 days (paired *t*-test, t = -1.69, *d.f.* = 11, *P* = 0.123), or one year (paired *t*-test, t = 0.25, d.f. = 7, *P* = 0.811). Initial condition also had no effect on weight gain from nestling to one year (paired *t*-test, t = -1.87, *d.f.* = 7, *P* = 0.103).

6.4.4 *Influence of satiation on behaviour*

Fledglings increased their time spent foraging, when on the ground, after their satiation level had been artificially increased through supplemental feeding (Figure 6.4 and Table 6.3; see Chapter 6 Appendix Table S6.2 for a list of all candidate models). Conversely, they reduced their investment in associations following supplemental feeding (Figure 6.5 and Table 6.4; see Chapter 6 Appendix Table S6.3 for a list of candidate models).

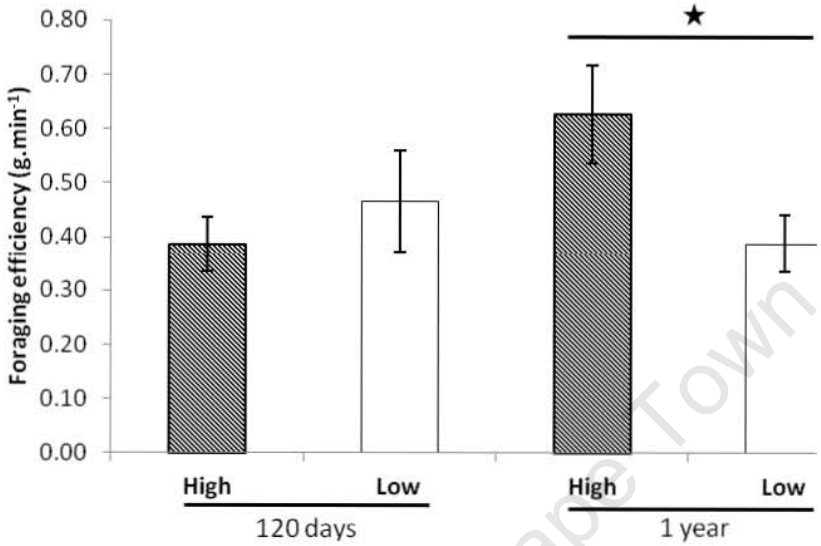

Figure 6.3 Influence of investment in foraging by juvenile pied babblers when young (50 days post-hatching) on foraging efficiency at 120 days and one year old. Data were collected from pairs of same-sex siblings. Individuals who invested more time in foraging at 50 days post-hatching were classified as high, while their siblings were classified as low. Foraging efficiency is presented as mean ± S.E. of raw data.

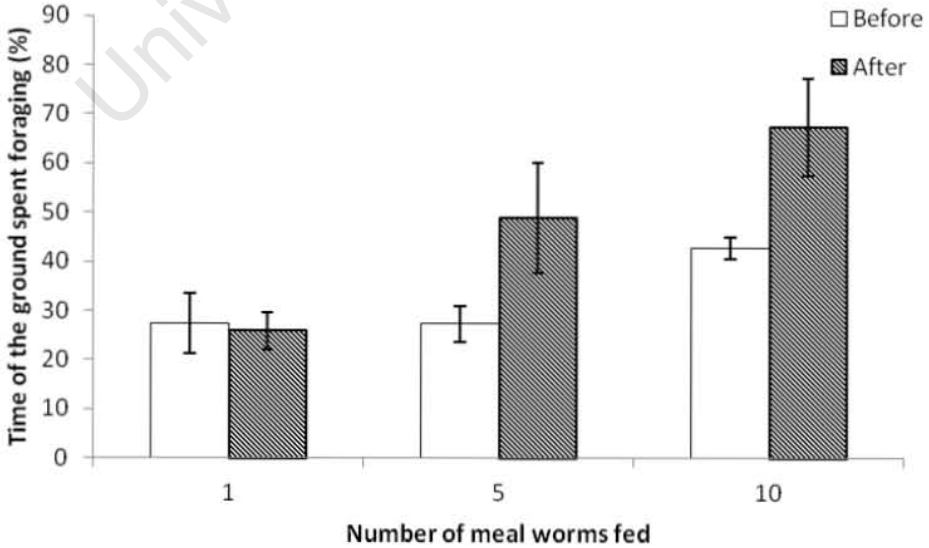

Figure 6.4 The influence of satiation on investment in foraging by fledgling pied babblers before and after being fed one, three or five supplemental meal worms. (Mean ± S.E. of raw data).

Table 6.3 Model selection on a series of GLMM models investigating the effect of hunger on fledgling investment in foraging. The response term was the arcsine-square-root of the proportion of time on the ground that fledglings spent foraging. Anum, Fsex and Fage are the same as listed above. Additional abbreviations: before = the focal before supplemental feeding (1, 5 or 10 worms); after = focal after supplemental feeding. All GLMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. Top five models are in presented. N = 96.

Model	Deviance	*K*	AICc	ΔAICc	w_i	Effect ± S.E.	
Focal*Worm number + Adult number	-161.5	9	-143.17	0.00	0.46	before*1	0.000 ± 0.000
						before*5	0.008 ± 0.073
						before*10	0.131 ± 0.071
						after*1	-0.010 ± 0.073
						after*5	0.121 ± 0.094
						after*10	0.209 ± 0.090
						Anum	-0.029 ± 0.011
Focal*Worm number + Adult number + Fledgling age	-161.8	10	-141.18	1.98	0.17	before*1	0.000 ± 0.000
						before*5	0.009 ± 0.086
						before*10	0.133 ± 0.084
						after*1	-0.010 ± 0.086
						after*5	0.121 ± 0.104
						after*10	0.211 ± 0.010
						Anum	-0.029 ± 0.011
						Fage	-0.0004 ± 0.0007
Focal*Worm number + Adult number + Fledgling sex	-161.5	11	-140.57	2.60	0.13	before*1	0.000 ± 0.000
						before*5	0.008 ± 0.074
						before*10	0.131 ± 0.072
						after*1	-0.010 ± 0.074
						after*5	0.120 ± 0.095
						after*10	0.209 ± 0.091
						Anum	-0.029 ± 0.011
						Sex:F	0.000 ± 0.000
						Sex:M	0.001 ± 0.020
Focal*Worm number	-154.9	8	-139.32	3.85	0.07	before*1	0.000 ± 0.000
						before*5	-0.0001 ± 0.056
						before*10	0.150 ± 0.053
						after*1	-0.010 ± 0.057
						after*5	0.113 ± 0.088
						after*10	0.228 ± 0.081
Focal*Worm number + Adult number + Fledgling age + Fledgling sex	-161.8	12	-138.52	4.65	0.05	before*1	0.000 ± 0.000
						before*5	0.008 ± 0.089
						before*10	0.133 ± 0.090
						after*1	-0.010 ± 0.089
						after*5	0.120 ± 0.090
						after*10	0.211 ± 0.090
						Anum	-0.030 ± 0.011
						Fage	-0.0004 ± 0.0007
						Sex:F	0.000 ± 0.000

						Sex:M	0.003 ± 0.024

Table 6.4 Model selection on a series of GLMMS models investigating the effect of hunger on fledgling investment in associations. The response term was the arcsine-square-root of the proportion of time on the ground that fledglings spent associating. All abbreviations are the same as listed previously. All GLMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. Top five models are in presented. N = 96.

Model	Deviance	*K*	AICc	ΔAICc	w_i	Effect ± S.E.	
Focal*Worm number + Fledgling number	-8.489	9	10.19	0.00	0.27	before*1	0.000 ± 0.000
						before*5	-0.071 ± 0.110
						before*10	-0.013 ± 0.105
						after*1	-0.128 ± 0.110
						after*5	-0.283 ± 0.133
						after*10	-0.300 ± 0.130
						Fnum	-0.046 ± 0.025
Focal*Worm number	-5.474	8	11.20	1.02	0.16	before*1	0.000 ± 0.000
						before*5	-0.062 ± 0.095
						before*10	0.002 ± 0.088
						after*1	-0.128 ± 0.095
						after*5	-0.274 ± 0.122
						after*10	-0.286 ± 0.117
Focal*Worm number +Adult number	-7.119	9	12.39	2.21	0.09	before*1	0.000 ± 0.000
						before*5	-0.057 ± 0.112
						before*10	-0.006 ± 0.107
						after*1	-0.128 ± 0.113
						after*5	-0.268 ± 0.137
						after*10	-0.294 ± 0.133
						Anum	-0.046 ± 0.025
Focal*Worm number +Fledgling age + Fledgling number	-8.536	10	12.45	2.26	0.09	before*1	0.000 ± 0.000
						before*5	-0.071 ± 0.125
						before*10	-0.014 ± 0.121
						after*1	-0.128 ± 0.125
						after*5	-0.282 ± 0.147
						after*10	-0.301 ± 0.143
						Fage	0.0002 ± 0.0013
						Fnum	-0.046 ± 0.025
Focal*Worm number +Fledgling sex	-6.386	10	12.85	2.66	0.07	before*1	0.000 ± 0.000
						before*5	-0.057 ± 0.096
						before*10	0.004 ± 0.090
						after*1	-0.128 ± 0.096
						after*5	-0.268 ± 0.123
						after*10	-0.272 ± 0.119
						Sex:F	0.000 ± 0.000
						Sex:M	-0.053 ± 0.042

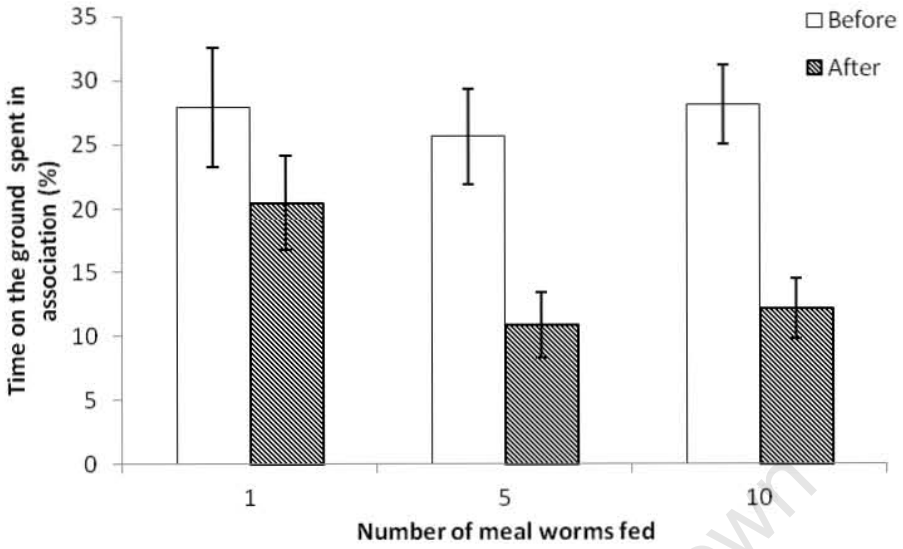

Figure 6.5 The influence of satiation on investment in associations by fledgling pied babblers before and after being fed one, three or five supplemental meal worms. (Mean ± S.E. of raw data).

6.4.5 *Initial investment in foraging on weight at one year*

There was no significant association between initial investment in foraging and increase in weight from nestling to weight at one year: mean for high foragers 35.44 g ± 1.62 g S.E. and for low foragers 34.9 g ± 1.36 g S.E. (paired *t*-test, t = 0.25, *d.f.* = 14, *P* = 0.810).

6.5 Discussion

For pied babbler fledglings, investment in foraging, and therefore individual-learning, appears to be the most important factor influencing foraging ability at one year. Fledglings who invested more time foraging than their same-sex broodmates developed higher foraging efficiency at one year. In contrast, fledglings with initially higher foraging efficiency, who were in better condition just prior to fledging or who exhibited higher investment in associations when young, did not develop significantly higher foraging efficiency than their siblings. The results of the feeding experiment are consistent with the natural data, demonstrating that a relaxation of energetic constraints resulted in fledglings investing in foraging (individual-learning) rather than associations. These results fit well with studies on cooperatively breeding meerkats (Thornton 2008a). Like meerkat pups, pied babbler fledglings invest time in foraging when their satiation levels were elevated. However, unlike

meerkats, there was no effect of initial condition on the proportion of time spent foraging by pied babbler fledglings.

Individual-learning is generally important in developing skills and behaviours. For example, juvenile Eurasian dippers (*Cinclus cinclus*) improve the coordination of their motor skills with age: stumbling less, capturing larger prey and handling it more efficiently (Yoerg 1994). In addition, individual-learning may be useful in honing socially acquired knowledge, by fine-tuning foraging techniques via trial-and-error learning (Laland & Plotkin 1992; Moscovice & Snowdon 2006). Pied babbler fledglings, like meerkat pups (Thornton 2008a), that invested in foraging early in life promoted the development of their foraging skills, potentially leading to long-term benefits. The effect on foraging ability was not seen at 120 days, but was detectable when offspring reached one year and may have been ready to disperse (Raihani et al. 2010). Like white-winged choughs, pied babbler fledglings may try to balance learning with acquiring sufficient food via begging (Heinsohn 1991), and when they are in a positive energetic state they may be able to afford to invest in an activity that benefits them in the long-term even with relatively low short-term gains. The results of this study are consistent with previous work on pied babbler fledglings, where fledglings try to maximize the provisioning benefits gained during a variable period of post-fledging care (Thompson & Ridley 2013).

It is not clear why some fledglings invested more in foraging during their dependent phase than others. Unlike Thornton's (2008a) study, there appeared to be no link between offspring condition and early investment in foraging. However, I was only able to measure nestling condition prior to fledgling and measures of fledgling condition may have given different results. The supplemental feeding experiment showed that investment in foraging was dependent on energetic constraints. Changes in offspring condition between fledging and 50 days post-hatching may thus have influenced investment in foraging. Unfortunately, I was unable to investigate condition during this period. Investment in foraging appeared to have no effect on individual increases in weight (from nestling to one year), as would have been predicted from the results of Ridley & Raihani (2007a). However, the weight difference found by Ridley & Raihani (2007a) was determined by duration of care, whereas these investigations were carried out on same-sex pairs from the same brood where the difference

in the duration of care between siblings is likely to be small (2.16 ± 0.44 days S.E.; Ridley & Raihani 2007a). Therefore, difference in weight due to foraging ability may be masked by siblings having similar length periods of care. A longer-term investigation into individual weights may have uncovered differences later in life, but these data were not available.

These results suggest that associations may not play a major role in social-learning and the development of foraging skills in pied babblers. Nevertheless, social-learning may be important for learning different aspects of foraging skills. Thornton & Hodge (2008) showed that social influences assisted in the development of foraging patch selection in meerkats. Similarly, associations in pied babblers may assist fledglings in learning where to forage. In support of this idea, young fledglings exhibited higher foraging efficiency when in association than when foraging alone, suggesting that associations may help fledglings locate productive food patches. The majority of pied babbler foraging involves excavation of subterranean invertebrates (Hollén et al. 2011; Child et al. 2012). This method of foraging may rely heavily on well-developed motor skills, thus individuals well practised in these skills may achieve a higher foraging efficiency. It is possible that individuals practice and improve their skills in behaviours that are learnt socially. For example, a foraging experiment carried out on Norway rats (*Rattus norvegicus*) showed that individuals who were given experience, following the observation of a trained demonstrator, had higher foraging success than those who only observed trained demonstrators (Laland & Plotkin 1992). Recent research on the tandem running ant (*Temnothorax albipennis*) has shown that a combination of social-learning and individual-learning is used to improve route use (Franklin & Franks 2012). It seems plausible that low levels of association would be sufficient to extract relevant information about when, what and where to eat (Galef & Giraldeau 2001), but that the refining of skills through practise may make a larger difference in learning how to catch prey. The interaction between social and individual-learning is supported by Thornton & McAuliffe's (2006) study of teaching in meerkats: adult meerkats provide pups with the opportunity to handle increasingly mobile prey, but pups' ability is improved via trial-and-error.

The lack of an effect of nestling condition on foraging skill development corroborates the findings of Ridley & Raihani (2007a), who did not find an effect of nestling body mass on

juvenile development. Combined with the result that initial foraging efficiency was not correlated with subsequent foraging ability (at 120 or 365 days), it suggests that developmental pathways in pied babblers are not fixed. The supplemental feeding experiment results give a glimpse into the mechanisms that individuals may use to alter their developmental trajectory. The increased investment in foraging observed in this study is in line with the results of previous work on pied babblers (A.R. Ridley unpublished data). Adult pied babblers apparently change their investment in different foraging techniques depending on their energetic state, investing more in time-intensive, high-risk, high-reward digging when nutritionally unconstrained (A.R. Ridley unpublished data). Taking these two pied babbler studies, together with other work (Davies 1976; Thornton 2008a), suggests that the mechanisms driving individual-learning are related to the ability to bear the costs of investing time in behaviours with long-term benefits but limited short-term benefits, with individuals only able to invest in individual-learning when the costs of doing so are reduced.

Prolonged post-fledging care can provide a risk free period (Langen 1996b), during which time adult provisioning allows fledglings to explore and practise foraging behaviours (Sullivan 1988; Heinsohn 1991). Ridley & Raihani (2007a) showed that foraging efficiency, adult body mass and dispersal in pied babblers were all affected by the duration of post-fledging care. Within the confines of the duration of post-fledging care, which is seemingly under adult control, this study shows that the investment fledglings put into individual-learning (via foraging) when they were young influenced their foraging ability when they were older. Therefore, offspring seemingly have the ability to maximize the development of their foraging skills within the confines of their dependent period.

Chapter 6 Appendix

Investigating the factors that affect foraging development

Full tables listing all candidate models tested

Deviance= -2log-likelihood output of each model; *K*= the number of parameters tested in each model; AIC= Akaike's information criterion; ΔAIC= the models AIC minus the minimum AIC among candidate models. For each candidate model: Basic= basic model with no predictor terms, only the constant, the random terms and residual variance (σ^2); Fage = fledgling age (days); $Fage^2$ = fledgling age^2; Fsex = fledgling sex (female or male); Anum = number of adults in the group; Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio; brood = brood number; rnfl.b4.hthc = cumulative rainfall for the two months preceding hatching; rnfl.b4.fl = cumulative rainfall for two months prior to the fledging; rnfl.b4.fcl = cumulative rainfall for two months prior to the focal. All GLMMs were fixed with individual identity and group identity as random terms to account for the potential influence of repeated measures on the distribution of data. All models with ΔAICc <5 are in bold.

Table S6.1: Factors affecting foraging efficiency ($g.min^{-1}$)

Model	Deviance	*K*	AIC	ΔAIC
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fnum + brood	-277	10	-257.0	0.0
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fnum	-274.8	8	-256.8	0.2
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + brood	-274.5	9	-256.5	0.5
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + ADFL	-274.2	8	-256.2	0.8
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch	-272	7	-256.0	1.0
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.fl + Fnum	-273.4	8	-255.4	1.6
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.fl + ADFL	-273.3	8	-255.3	1.7
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.fl + brood	-272.9	9	-254.9	2.1
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fnum + Anum	-274.8	9	-254.8	2.2
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.fl	-270.5	7	-254.5	2.5
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Anum	-272.2	8	-254.2	2.8
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.fl + Anum	-270.9	8	-252.9	4.1
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fnum + Fsex	-267.6	10	-247.6	9.4
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fsex	-265.2	9	-247.2	9.8
Fage + Fage² + rnfl.b4.fcl + brood	-263	8	-247.0	10.0
Fage + Fage² + rnfl.b4.fcl + rnfl.b4.htch + Fsex	-263.5	9	-245.5	11.5
Fage + Fage² + rnfl.b4.fcl	-251.9	6	-237.9	19.1
Fage + Fage² + rnfl.b4.fcl + ADFL	-253.5	7	-237.5	19.5
Fage + Fage² + rnfl.b4.fcl + Fnum	-252.9	7	-236.9	20.1
Fage + Fage² + rnfl.b4.fcl + Anum	-252.4	7	-236.4	20.6
Fage + Fage² + rnfl.b4.fcl + Fsex	-245.2	8	-229.2	27.8
Fage + Fage² + brood	-219.4	7	-205.4	51.6
Fage + Fage² + rnfl.b4.htch	-217	6	-203.0	54.0
Fage + Fage² + Anum	-214.8	6	-200.8	56.2
Fage + Fage² + rnfl.b4.fl	-214.8	6	-200.8	56.2
Fage + Fage²	-211.2	5	-199.2	57.8
Fage + Fage² + Fnum	-212.3	6	-198.3	58.7

Fage + Fage² + ADFL	-212.2	6	-198.2	58.8
Fage + Fage² + Fsex	-203.4	7	-189.4	67.6
Fage	-141.8	4	-131.8	125.2
rnfl.b4.fl + Fnum + Anum	126.7	7	140.7	397.7
rnfl.b4.fl + brood	129	7	141.0	398.0
rnfl.b4.htch + Fnum + Anum	127.5	7	141.5	398.5
rnfl.b4.fcl + Fnum + Anum	128.2	7	142.2	399.2
rnfl.b4.htc + Fnum	128.2	6	142.2	399.2
rnfl.b4.fl + Anum	130.5	6	142.5	399.5
ADFL	133.1	4	143.1	400.1
Anum	133.2	4	143.2	400.2
rnfl.b4.fl + ADFL	131.4	6	143.4	400.4
rnfl.b4.htch + ADFL	132.3	6	144.3	401.3
rnfl.b4.fcl + ADFL	132.7	6	144.7	401.7
rnfl.b4.htch + brood	132.9	7	144.9	401.9
rnfl.b4.fcl + Anum	133	6	145.0	402.0
rnfl.b4.fl + Fnum	135.9	6	147.9	404.9
Fnum	138.1	4	148.1	405.1
rnfl.b4.fl + Fsex	136.4	7	148.4	405.4
Fsex	138.9	5	148.9	405.9
rnfl.b4.htch + Anum	137	6	149.0	406.0
rnfl.b4.fcl + Fnum	137.1	6	149.1	406.1
brood	139.5	5	149.5	406.5
rnfl.b4.fcl + Fsex	137.9	7	149.9	406.9
rnfl.b4.htch + Fsex	138	7	150.0	407.0
rnfl.b4.fl	140.2	4	150.2	407.2
rnfl.b4.fcl + brood	138.5	7	150.5	407.5
basic	143.5	3	151.5	408.5
rnfl.b4.htch	142	4	152.0	409.0
rnfl.b4.fcl	142.6	4	152.6	409.6

Table S6.2: Effects of feeding on proportion of time on the ground fledgling spent foraging

Model	Deviance	*K*	AICc	ΔAICc
F*W+Anum	-161.5	9	-143.2	0.0
F*W+Anum+Fage	-161.8	10	-141.2	2.0
F*W+Anum+Fsex	-161.5	11	-140.6	2.6
F*W	-154.9	8	-139.3	3.8
F*W+Anum+Fage+Fsex	-161.8	12	-138.5	4.6
F*W+ADFL	-155.5	10	-137.2	6.0
F*W+Fage	-154.9	9	-137.1	6.1
F*W+Fnum	-154.9	9	-137.1	6.1
F*W+Fsex	-154.9	10	-136.8	6.4
F*W+Fage+Fsex+Anum+Fnum	-161.9	13	-136.2	6.9
F*W+Fage+ADFL	-155.5	11	-134.9	8.3
F*W+Fage+Fnum	-154.9	10	-134.8	8.4
F*W+Fsex+ADFL	-155.5	12	-134.5	8.6
F*W+Fage+Fsex	-154.9	11	-134.5	8.7
F*W+Fsex+Fnum	-154.9	11	-134.5	8.7
F*W+Fage+Fsex+Fnum	-154.8	12	-132.2	10.9
F*W+Fage+Fsex+ADFL	-155.5	13	-132.1	11.0
Anum	-122.7	4	-112.4	30.7
Anum+Fnum	-123.5	5	-111.1	32.1
Fsex+Anum	-123	6	-110.4	32.7
Fage+Anum	-122.8	5	-110.4	32.8
Fsex+Anum+Fnum	-123.8	7	-109.1	34.0
Fage+Anum+Fnum	-123.5	6	-109.0	34.1
Fage+Fsex+Anum	-123	7	-108.3	34.8
Fage+Fsex+Anum+Fnum	-123.8	8	-106.9	36.2
basic	-111.2	3	-103.1	40.0
Fnum	-112.2	4	-102.0	41.1
Fage	-111.6	4	-101.3	41.8
ADFL	-111.5	5	-101.2	42.0
Fsex	-111.4	5	-101.0	42.2
Fage+Fnum	-112.4	5	-100.1	43.1
Fsex+Fnum	-112.5	6	-100.0	43.1
Fage+ADFL	-111.9	6	-99.4	43.7
Fage+Fsex	-111.7	6	-99.2	44.0
Fsex+ADFL	-111.6	7	-99.0	44.2
Fage+Fsex+Fnum	-112.6	7	-98.0	45.2
Fage+Sex+ADFL	-112.0	8	-97.1	46.0

For this table Deviance, *K*, Fsex and Fage are all the same as listed above. AICc= Akaike's information criterion for small data sets; ΔAICc= the models AICc minus the minimum AICc among candidate models. F*W = the interaction between focal (before or after) and number of supplemental worms

fed (1, 5 or10); Anum = number of adults in the group; Fnum = number of fledglings in the group; ADFL = adult:fledgling ratio.

Table S6.3: Effects of feeding on proportion of time on the ground fledgling spent in association

Model	Deviance	*K*	AICc	ΔAICc
F*W+Fnum	-8.489	9	10.2	0.0
F*W	-5.474	8	11.2	1.0
F*W+Anum	-7.119	9	12.4	2.2
F*W+Fage+Fnum	-8.536	10	12.4	2.3
F*W+Fsex	-6.386	10	12.8	2.7
F*W+Fsex+Fnum	-8.593	11	13.3	3.1
F*W+Fage	-5.544	9	13.4	3.2
F*W+ADFL	-5.44	10	13.6	3.4
F*W+Fsex+Anum	-7.944	11	14.2	4.0
F*W+Fage+Anum	-7.145	10	14.7	4.5
F*W+Fage+Fsex	-6.45	11	15.1	5.0
F*W+Fage+Fsex+Fnum	-8.609	12	15.1	5.0
F*W+Fsex+ADFL	-6.331	12	15.4	5.2
F*W+Fage+ADFL	-5.412	11	16.1	6.0
F*W+Fage+Fsex+Anum+Fnum	-10.53	13	16.3	6.1
F*W+Fage+Fsex+Anum	-7.937	12	16.5	6.3
F*W+Fage+Fsex+ADFL	-6.346	13	17.7	7.5
Fsex	23.39	5	33.7	23.5
basic	26.35	3	34.5	24.3
Fsex+Anum	22.28	6	34.8	24.7
Fsex+Fnum	22.48	6	34.9	24.7
Fnum	24.82	4	35.0	24.8
Anum	25.33	4	35.6	25.4
Fage+Fsex	23.4	6	35.9	25.7
Anum+Fnum	23.63	5	36.0	25.8
Fsex+ADFL	23.45	7	36.1	25.9
Fsex+Anum+Fnum	21.55	7	36.1	25.9
Fage	26.35	4	36.6	26.4
ADFL	26.35	5	36.8	26.6
Fage+Fsex+Anum	22.42	7	37.0	26.8
Fage+Fnum	24.82	5	37.1	26.9
Fage+Fsex+Fnum	22.49	7	37.2	27.0
Fage+Anum	25.32	5	37.7	27.5
Fage+Anum+Fnum	23.6	6	38.2	28.0
Fage+Fsex+ADFL	23.47	8	38.3	28.1
Fage+Fsex+Anum+Fnum	21.54	8	38.3	28.1
Fage+ADFL	26.35	6	38.9	28.7

Table S6.4: Predictor weights for all variables investigating factors affecting fledgling foraging efficiency ($g.min^{-1}$)

Predictor terms	Weight
Fledgling age (days)	**1**
Fledgling age^2	**1**
Rainfalll before focal	**1**
Rainfall before hatching	**0.734**
Fledgling number	0.434
Rainfall before fledging	0.265
Brood number	0.344
Adult:fledgling ratio	0.177
Adult number	0.114
Fledgling sex	0.003

Predictor weights for the all variables investigated in LMMs. Predictor weights for each variable were calculated by summing the Akaike weights for each model that contained that variable (Symonds & Moussalli 2011). Variables that appear in all the top models will have weights that tend towards 1 and if variables only appear in unlikely models their weight will tend towards 0 (Symonds & Moussalli 2011). All variables deemed to be important are in bold.

Table S5. Predictor weights for all explanatory variables used in the models to investigate the effects of feeding on proportion of time on the ground fledgling spent foraging and in association. All variables deemed to be important are in bold.

	Weight	
Predictor terms	**Foraging**	**Association**
Focal (Before/After) * Worm number	**0.999**	**0.999**
Adult number	**0.812**	0.176
Fledgling age (days)	0.275	0.255
Fledgling sex	0.224	0.257
Fledgling number	0.051	0.443
Adult:fledgling ratio	0.038	0.088

Chapter 7

General discussion

General discussion

7.1 Overview

The period of an individual's life where they are dependent upon adult care-givers for nutrition has the potential to shape their life-history trajectory (Alonso-Alvarez et al. 2006; Ridley & Raihani 2007a; Lee et al. 2013). These long-term impacts will play a role in familial conflicts, as both care-givers and offspring seek their own optimal distribution of resources that maximizes their fitness (Trivers 1974). By investigating offspring begging behaviour it is possible to understand these familial conflicts and their resolutions. Begging can take many forms (Kilner 1997; Rauter & Moore 1999; Saino et al. 2000; Tanaka & Ueda 2005; den Boer & Duchateau 2006) and be carried out in a variety of environments (Weygoldt 1980; Kilner 1995; Smiseth et al. 2003; Bell 2007). The majority of investigations into begging behaviour have used nestling birds as their model system (Kunc et al. 2007). However, more studies have started to investigate begging behaviour in species with mobile offspring (Smiseth et al. 2003; Bell 2008a; English et al. 2008). By studying the begging behaviour of fledgling pied babblers, I have been able to expand on this work to show commonalities between the begging systems of mobile offspring. I investigated the dynamics of fledgling solicitation, focusing on the structure, function and use of fledgling begging, the role of risk in solicitation and also investigated the long-term effects of dependence.

7.2 How pied babbler fledgling begging works

The results of this study suggest that the begging system of fledgling pied babblers is simple and apparently primarily affected by hunger and not sibling' begging effort. Thus, fledgling begging is a reliable signal of hunger level (Chapter 4), with hungrier individuals investing more time in begging and individual fledglings' begging behaviour being independent of the begging of broodmates. Adult provisioning appears to be positively related to the amount of time fledglings invest in begging. In addition, adults are able to increase their provisioning efforts in such a way as to allow them to increase provisioning to offspring who are begging more while maintaining provisioning to the rest of the brood. Therefore, fledgling begging in

this species appears to be a reliable signal of hunger that care-givers use to allocate resources.

7.3 Information in solicitation

7.3.1 *Need*

In Godfray's (1991) model of offspring signalling, offspring's need was cryptic and the neediest offspring stood to gain the most from provisioning. Therefore, begging was an honest signal of offspring need (Godfray 1991; Godfray 1995). Need refers to the fitness benefit that offspring stand to gain from additional investment. Since this is difficult to quantify and measure empirically, most studies use hunger as a proxy for need (Johnstone & Kilner 2011). The results from this thesis show that the solicitation behaviours of pied babbler fledglings are effective and reliable ways to convey offspring hunger to adult care-givers. Fledglings use multiple modes to signal their need: acoustic structure of calls (Chapter 3), time spent emitting begging calls (Chapter 4) and their location (Chapter 5). Firstly, hunger was encoded in the structure of begging calls (Chapter 3), as changes in satiation resulted in changes to the acoustic structure of begging calls. It remains to be tested whether adults use this cue to adjust their provisioning effort or in choosing which fledgling to provision. Hunger is encoded in the structure of begging calls of other species as well (Leonard & Horn 2006; Manser et al. 2008; Anderson et al. 2010). For example, adult meerkats preferentially feed speakers which play back calls of hungry pups over those which play calls of satiated pups (Manser et al. 2008). Secondly, investment in begging, in terms of the proportion of time that fledglings spent vocalizing (Chapter 4), was a reflection of hunger. Begging investment was negatively related to satiation, with experimentally fed fledglings spending less time begging. The results of this experiment are supported by the fact that recent rainfall, a proxy for food availability (Cumming & Bernard 1997), was also a significant negative factor predicting the begging behaviour of fledglings (Chapter 3). The relationship between hunger and begging in fledgling pied babblers is consistent with the results of many other studies (reviewed in Mock et al. 2011), where offspring reduce their begging investment when they are more satiated. This relationship between begging and satiation follows a negative "effect of supply on demand" (ESD) function (Grodzinski & Johnstone 2012). The cost of care is important in determining how adults respond to offspring begging. Grodzinski & Johnstone (2012) demonstrated that care-givers will tend to

show a negative ESD when the cost of allocation in the system is low, because as the cost of care increases adults are predicted to become less responsive to offspring begging and so begging becomes less effective. Thus, the negative ESD suggests that the cost of care may be low in this system. Finally, young fledgling pied babblers were able to use their location to signal their level of hunger (Chapter 5). Experimentally satiated fledglings spent more time in the safety of trees while hungrier fledglings moved to the ground, where they were provisioned at higher rates.

Taking all of these factors together it appears that fledglings are able to take advantage of multiple modes of signalling to convey hunger to care-givers (Johnstone 1996a). It is not surprising that various solicitation displays convey need, as ensuring receipt of resources is crucial for offspring survival. Multiple signals conveying hunger suggests that the solicitation behaviour of pied babblers falls in line with Johnstone's (1996a) 'backup signals' hypothesis, resulting in a signalling system that contains redundancy (Møller & Pomiankowski 1993; Johnstone 1996a). Multiple signals may also aid in efficient information transfer by increasing signal detection (Jacob et al. 2011), although this is not a mutually exclusive hypothesis. Further investigation will allow an analysis of how these signals interact and their relative importance.

7.3.2 *Identity*

In Chapter 3, I show that the begging calls of fledgling pied babblers were individually distinguishable. The existence of individually distinct calls in provisioning interactions have been found to be important for parents to correctly locate their offspring in a number of colonial species (Jouventin et al. 1999; Page et al. 2002; Charrier et al. 2002). This is advantageous in such systems because several families typically live in close proximity meaning that there is a relatively high chance of feeding an unrelated chick by mistake. Pied babblers are territorial and live in tight-knit family groups (Golabek et al. 2012) and so are not subject to the same selection pressures as colonial species. There may still be advantages for parents to identify individual offspring however.

It is possible that adults use the identity information encoded in fledgling begging calls to allocate food delivery among the brood. When offspring are confined to a closed space, for

example a nest, care-givers may be able to easily determine who to provision by comparing closely located offspring directly. When offspring are mobile, as is the case for pied babbler fledglings and many other species, adults may be unable to directly compare offspring (Manser et al. 2008). Adult pied babblers do not always have a fledgling associating with them and fledglings frequently move between foraging partners (described as social-foraging in Thompson & Ridley (2013)). The 'repeat' begging calls that fledglings give outside feeding events (Chapter 3) may signal the current hunger level of that fledgling to adults and identify which fledgling the call belongs to. Under these circumstances, fledglings may benefit from producing individually identifiable calls if adults keep track of different fledglings in the group and seek out the hungriest chick when they find a food item. When care-givers increase their provisioning it does appear to only be allocated to those fledglings that increase their begging (Chapter 4). However, it is unclear if this is simply done by feeding the fledgling who begs the most or whether recognition of individual calls plays a part. This is because adult pied babblers tend to provision the closest fledgling (Thompson & Ridley 2013) and may simply be following a rule to feed the closest fledgling with the most intense begging. To determine if adults use individuality in calls to influence provisioning decisions, future work could use experiments similar to those used in Chapter 4. Three different playback treatments could be used: playback of the focal fledglings begging; playback of a sibling's begging; and playback of the begging of a fledgling from another group. If adult provisioning response differs between these treatments, it would suggest that individual identity in call structure affects allocation.

An alternative, and perhaps more parsimonious explanation, is that individually distinct calls may simply be a morphological by-product and are not used to inform adult provisioning decisions. Individual differences in vocalizations may be generated by physiological or morphological differences between fledglings, as factors such as body size are known to influence call structure (Zweifel 1968; Davies & Halliday 1978; Wagner 1989; Fitch 1997). It has been proposed that the calls used by adult birds develop from offspring begging calls (Redondo & Exposito 1990). A variety of studies have shown individuality in calls and individual recognition (reviewed in Tibbetts & Dale 2007). The advantages of individual recognition in group living species may be particularly large, as individuality in calls may be

useful for kin recognition, assisting in inbreeding avoidance and helping decisions, as well as aggressive interactions (Tibbetts & Dale 2007). Other cooperatively breeding species have been shown to produce individual specific calls and show individual recognition (Sharp et al. 2005; Townsend et al. 2012). Individuality in fledgling begging calls may be a step in the vocal ontogeny that leads to individually distinct adult calls. The adult calls of pied babblers are highly likely to be individual, with current research being conducted showing that territory overlap is greatest between groups with a related dominant (D. Humphries unpublished data) and individual recognition is a key requirement of this trend.

7.3.3 *Distinct call types*

The signalling behaviour of animals has been demonstrated to be influenced by social and environmental factors (Grodzinski et al. 2007; Ey & Fischer 2009; Fairhurst et al. 2013). A number of studies have shown that animal calls are used in specific context and contain information: using different alarm calls depending on the type of predator (Seyfarth et al. 1980; Manser 2001b); altering call rate in relation to predation risk (Bell et al. 2010; Townsend et al. 2011); and using different call types in inter or intragroup contexts (Golabek & Radford 2013). Much of this work has focused on alarm and food calling (Seyfarth et al. 1980; Dittus 1984; Elgar 1986; Manser 2001b). Previous research has suggested that multiple begging calls may be a behavioural adaptation selected for when offspring are mobile (Manser & Avey 2000; Madden et al. 2009a). Therefore, mobility might lead to the evolution of commonalities in the features and use of begging calls in mobile offspring. In Chapter 3, I show that, like mobile meerkat pups (Manser & Avey 2000; Kunc et al. 2007), fledgling pied babblers have two types of begging call: crescendo begs and repeat begs. Analysis of the use of these calls demonstrated they were used in specific contexts: with crescendo calls used much closer to feeding events and repeat calls outside of feeding events. These two begging call types are analogous to two of the begging calls used by meerkat pups, with babbler crescendo calls akin to meerkat high-pitched calls and babbler repeat calls akin to meerkat repeat calls (Manser & Avey 2000; Kunc et al. 2007). Begging can serve two functions: to influence the level of provisioning or to influence the allocation of provisioning (Johnstone 2004). The context in which crescendo and repeat calls occur suggests that each might serve one of these two functions. Repeat calls may be used to signal fledgling hunger and to influence adult provisioning rate; while crescendo calls may

primarily serve to determine the allocation of food among the brood. Investigation into the function of high-pitched and repeat calls in meerkats appears to support this hypothesis (Kunc et al. 2007; Manser et al. 2008). Nevertheless, further analysis of crescendo and repeat begs needs to be done because the experiments I carried out could not find any difference in adult response to these two call types. This is potentially due to my experimental design not testing the use of these call types in the correct ecological context. A simple choice test put to adults would be able to determine if this is the case, similar to that used by Kunc et al. (2007). If it was shown that these different begging calls needed to be used in the correct context to elicit the correct response it would prove fruitful in understanding the evolution of communication (Crockford & Boesch 2003; Slocombe & Zuberbühler 2005).

To conclusively show that multiple begging call types are adaptation to a mobile lifestyle would necessitate comparing fledgling begging with those produced by nestlings. If mobility selects for multiple call types then I would expect these calls to only develop post-fledging. Nestling begging can occur outside of feeding events but it is likely to have little influence on parental provisioning rates if parents are not there to hear it (Leonard & Horn 2001a), and has instead been explained as a form of negotiation between nestlings (Roulin et al. 2000). Furthermore, signalling outside feeding events may be prohibitively risky for nestlings as begging may increase the risk that a predator will detect the nest (Haskell 1994; Leech & Leonard 1997). Although I was not able to test this hypothesis directly, previous work on this species has shown that fledglings experience lower predation risk than nestlings (Raihani & Ridley 2007b), perhaps for this reason. The primary opportunity for nestlings to directly signal to their care-givers is during the relatively short period around feeding events. Therefore, nestling begging calls are predominantly used to influence allocation (Leonard & Horn 2001a). I predict that the call type used by nestling pied babblers would be more similar to the crescendo begging calls of fledglings than to the repeat calls, but with insufficient high-quality recordings of nestling begging I was unable to test this hypothesis. If crescendo calls are used to influence allocation of resources, then according to Johnstone's (2004) theory, we might expect these calls to be more likely to escalate in response to increased signalling effort from siblings. I did not test this hypothesis but this would be a fruitful avenue for further research.

7.4 Adult response

Increasing begging investment will only be profitable if doing so results in care-givers increasing their feeding rates, allowing offspring to offset the cost of additional begging (Grodzinski & Johnstone 2012). As such, understanding how care-givers respond to offspring begging, the "effect of demand on supply", is a crucial aspect of understanding the drivers behind begging (Royle et al. 2004). To determine the function of begging it is crucial to understand the benefits that offspring gain from performing the behaviour. Pied babbler adults' provisioning was positively correlated with offspring begging, resulting in a positive "effect of demand on supply" (Chapter 4). This response is similar to that of many other species, although there are notable exceptions (Kölliker et al. 2000; Thorogood et al. 2011). The provisioning response of adult pied babblers was targeted, increasing allocation to those who begged more and reducing it to fledglings who begged less, while maintaining allocation levels to the rest of the brood (Chapter 4). In some species, when one individual increases its begging, the whole brood receives increased provisioning whereas if one individual reduces their begging, the whole brood receives reduced provisioning (Mathevon & Charrier 2004; Bell 2007). However, in pied babblers that is not the case. With offspring accompanying the foraging group, as fledgling pied babblers do, adults may be better able to assess individual begging levels, potentially reducing any reliance on the total begging effort of the brood. It is puzzling that banded mongoose pups also associate with adults, yet adult provisioning in this species appears to respond to the overall begging rate (Bell 2007). Clearly, further work is needed to determine what factors influence whether care-givers attend to total brood begging or the begging of specific individuals.

One potential factor that explains the pattern of resource allocation observed in this system is the dispersed nature of offspring and the presence of multiple care-givers. Offspring are able to spread out and follow individual adults, potentially reducing physical competition between siblings (Appendix 1). The allocation of resources by parents to nestling birds has been found to be in response to the outcome of physical competition in many studies (Rydén & Bengtsson 1980; Smith & Montgomerie 1991; Kacelnik et al. 1995; Kilner 2002b). Once chicks leave the nest they are no longer in such close proximity, potentially reducing

the importance of physical competition in affecting resource allocation (Appendix 1). Hence, in this system care-giver provisioning is more likely to be determined by begging investment rather than by the outcome of physical competition. However, pied babbler adults do tend to provision the closest fledgling (Thompson & Ridley 2013) and so physical competition may exist over access to adults. In pied babbler groups there are typically more care-givers than fledglings and fledglings rarely socially-forage with the same adult as another sibling (Appendix 1), possibly explaining why instances of direct physical competition between fledglings were relatively rare (A. Thompson personal observation). Furthermore, species with multiple care-givers may be better placed to increase provisioning to match demand, due to helpers decreasing the cost of care per individual (Hatchwell 1999; Meade et al. 2010). Thus, physical competition between siblings may be reduced in species with multiple care-givers.

An additional factor that may influence care-giver responsiveness to fledgling begging is the increase in predation risk that adults incur due to fledgling begging. As fledglings accompany the foraging group, their conspicuous begging calls may alert potential predators to the group's location (Haskell 1994). Adults have been shown to alter their vigilance behaviour in the presence of mobile begging offspring, as highlighted in recent work on meerkats (Santema & Clutton-Brock 2013). Adults may additionally reduce this cost by provisioning begging offspring to reduce their begging level (Chapter 4) and thus reduce the risk of attracting predators (Haskell 1994). The existence of this potential cost needs to be verified, as it may play a bigger role in systems with mobile rather than sedentary offspring.

7.5 Sibling response

Understanding how siblings respond to each other's begging is crucial in understanding the function of begging, whether it is used to influence food delivery or allocation (Johnstone 2004). Offspring can respond to changes in the begging behaviour of their siblings in a competitive or cooperative way, or alternatively their begging behaviour could be independent of the behaviour of siblings (Johnstone 2004). If begging is competitive, offspring escalate their investment in response to increased begging by their siblings, in an effort to gain access to a limited supply of resources (Royle et al. 2002; Johnstone 2004). Conversely, in cooperative begging, care-givers' provisioning levels are determined by the

collective signalling of offspring and so each individual may gain from the begging investment of its siblings (Johnstone 2004; Bell 2007). However, if offspring begging is not affected by the begging of siblings but only by internal factors such as hunger or condition, then begging is likely to be a reliable signal (Godfray 1995; Godfray & Johnstone 2000). The results of Chapter 4 show that the begging of pied babbler fledglings was not affected by the begging behaviour of their siblings; only hunger level affects their investment in begging. This result, combined with the other findings that time spent begging was related to hunger (Chapter 4), that hunger was encoded in the structure of begging calls (Chapter 3) and influenced fledglings' location (Chapter 5), suggest that fledgling acoustic begging may be a reliable signal of hunger in this species. The main reason why fledglings did not alter their begging in response to the begging of their siblings appears to be the response of adult care-givers. Firstly, adults were able to adjust their provisioning rates when an individual's begging was increased. Therefore, offspring were not competing over a fixed amount of resources and so did not need to escalate their begging (Parker et al. 2002; Royle et al. 2002). Secondly, the increased provisioning was targeted to manipulated fledglings, while provisioning rates were maintained towards control fledglings. Thus, fledglings gained no provisioning benefit nor suffered reduced provisioning due to the increased begging of their siblings (Johnstone 2004; Mathevon & Charrier 2004; Bell 2007). These results suggest that acoustic begging in fledgling pied babblers influences both the amount of food delivered to the brood and its allocation (Chapter 4).

A key component of POC and begging theory is the relatedness between siblings, both current and future (Trivers 1974; Grafen 1990; Godfray 1991; Godfray 1995). Begging behaviour is predicted to escalate as relatedness between siblings decreases, as indirect fitness benefits reduce (Parker et al. 1989; Briskie et al. 1994). The breeding system of pied babblers results in highly skewed reproductive success in favour of the dominant pair, who produce over 95% of all offspring (Nelson-Flower et al. 2011). Therefore, offspring are highly likely to be full siblings. The majority of pied babbler helpers are retained offspring (Ridley & Raihani 2008), thus the high probability that fledglings are highly related to their broodmates and care-givers implies that indirect kin selection benefits are likely to reduce the benefits of exaggerated (dishonest) begging.

7.6 Blackmail

Determining which party has control over provisioning is crucial in understanding the mechanisms behind the conflict over investment (Parker et al. 2002; Royle et al. 2002; Kilner & Hinde 2008). Due to the physical difference between care-givers and offspring, offspring are often the weaker party in these interactions and are thus expected to have limited control over adult provisioning behaviour. Identifying situations in which offspring can win these conflicts is critical to developing our understanding of POC (Mock & Forbes 1992). The mobility of fledglings offered a unique opportunity to explore a situation where offspring may have the upper hand. Zahavi (1977b) proposed that offspring could exploit the predation cost associated with begging to blackmail parents into feeding at higher levels than they would otherwise be prepared to. Experimentally testing this hypothesis requires a situation in which the response of parents to solicitation under different predation risks can be measured. Fortuitously, the mobility of fledgling pied babblers provides this opportunity. In this species, fledglings are more vulnerable to predators when they are on the ground than when they reside in the safety of trees. By moving to the ground, fledglings were able to manipulate care-givers into increasing their provisioning rates and investing time leading them back to the safety of the trees (Chapter 5). Movement to the ground forms an addition part of the signalling system employed by fledglings, along with acoustic begging (Chapters 3 & 4). Movement to the ground was linked with offspring hunger, with hungrier offspring willing to accept higher risks, and may therefore be seen as a signal of need. However, blackmail and signalling explanations of solicitation are not mutually exclusive (Godfray & Johnstone 2000).

The results of Chapter 5 highlight the fact that parent-offspring conflict is dynamic (Royle et al. 2002). As offspring get older, their mobility and ability to respond to alarm calls improves, resulting in movement to the ground becoming less effective at eliciting provisioning (Chapter 5). Changes that occur throughout development and environmental factors lead to POC being dynamic, with control over allocation, the costs of provisioning and the cost of signalling potentially changing. This is an important fact that needs to be considered in future research. This work also emphasizes that solicitation can occur over

many more contexts than those traditionally studied in avian begging research. The struggle over investment may take many different forms over the course of offspring dependence, with parents and offspring gaining control at different points. With the outcome of parent-offspring-conflict being influenced by many environmental and social factors (Royle et al. 2002), investigations should to be carried out in as many contexts as possible.

7.7 How fledglings influence their development

The period of nutritional dependence offers offspring the ideal situation in which to learn and develop the skills they will need in later life (Langen 1996; Thornton & McAuliffe 2006). The duration of this nutritionally dependent period can have long-term consequences for offspring survival and development (Heinsohn 1991; Langen 2000; Ridley & Raihani 2007a). Pied babblers can have overlapping broods of dependent young, and may be feeding a second brood of nestlings while first brood fledglings are still nutritionally dependent (Raihani & Ridley 2008b; Ridley & Raihani 2008). This commonly results in a shortened period of care for first brood offspring (Ridley & Raihani 2008). The length of offspring dependence in pied babblers is primarily determined by the cost of care to adult care-givers (Ridley & Raihani 2007a). Larger groups are better able to cope with the costs of care (Ridley & Raihani 2007a), as in many cooperative species increased groups size results in lower costs of care per individual (Hatchwell 1999; Russell et al. 2007a; Russell et al. 2008; Meade et al. 2010). As such, pied babbler fledglings have to maximize the development of their foraging skills within a limited and variable time period. To understand the ways in which fledglings might be able to maximize their foraging development, I asked what behaviours they invested in while nutritionally unconstrained. Firstly, fledglings reduced their predation risk (Chapter 5): satiated fledglings spent longer in the safety of trees (Ridley et al. 2013). Secondly, fledglings spent less time in association with foraging care-givers, and more time in individual-learning behaviours, foraging (Chapter 6). Increased investment in foraging is not necessarily the most immediately profitable behaviour, as fledglings typically have poor foraging skills (Chapter 6) (Heinsohn 1991; Yoerg 1994). However, as Chapter 6 and other studies (Thornton 2008a) have shown, investment in foraging when young can have long-term benefits. This behavioural change is not restricted to fledglings, as adults who are supplementally fed switch from a low-risk-low-reward foraging strategy to a high-risk-high-

reward strategy which may also aid in foraging skill development (A.R. Ridley unpublished data).

Individual-learning and social-learning have been proposed as ways for individuals to develop their foraging skills (Laland & Plotkin 1992). The results of Chapter 6 show that investment in individual-learning when young was the primary predictor of adult foraging efficiency in this species. However, these results do not preclude social-learning from being a crucial part of foraging development in pied babblers. This species has already been shown to use teaching (Raihani & Ridley 2008a) and the use of recruitment calls by adults, which are used to attract nutritionally independent offspring to divisible food sources, could aid in learning via local enhancement (Radford & Ridley 2006). The foraging efficiency of young fledglings was higher when they were simultaneously associating than when they were foraging alone (Chapter 6), suggesting a potential role for associations in learning the location of foraging patches. A number of studies have shown that social-learning is used in learning the location of foraging patches (Midford et al. 2000; Reader et al. 2003; Thornton & Malapert 2009), but the ability to utilize those patches may rely on skills learnt through individual-learning. However, further investigation is needed to determine the function of social-learning in pied babblers. Many other cooperatively breeding species have similar forms of prolonged care (McGowan & Woolfenden 1990; Langen 2000; Gilchrist 2004; English et al. 2008) and the results from my study suggest that investment in foraging when offspring are nutritionally unconstrained could be a mechanism commonly used by young to develop their foraging skills.

7.8 Future work

Recent literature has pointed out that the control over allocation between care-givers and offspring may lie on a continuum and is likely to change over the course of dependence, due to the dynamics of development (Royle et al. 2002). There are increasing calls for theoretical models to include more dynamic adult-offspring interactions (Godfray & Johnstone 2000; Royle et al. 2002; Shizuka & Lyon 2013). In addition, recent research on hihi (*Notiomystis cincta*) (Thorogood et al. 2011) and American coots (*Fulica americana*) (Shizuka & Lyon 2013) has shown that the optimal provisioning behaviours of parents are not fixed. These studies highlight that both environmental and developmental factors alter the optimum

behaviours of adults. The prolonged post-fledgling care exhibited in cooperatively breeding birds (Langen 2000) offers an ideal situation in which to investigate and compare adult-offspring interactions at different developmental stages. In order to build on the work I have already carried out, I would investigate the factors that affect begging behaviour and care-giver response in nestlings and during the period where care for fledgling is being terminated. Firstly, this would enable a direct within-species comparison of offspring in two different environments, nestling and fledgling phase. Secondly, conflict is likely to be most pronounced at the point where care is being terminated (Trivers 1974), thus enabling me to disentangle how offspring environmental and developmental differences affect offspring begging.

My study was carried out during a period absent of extreme weather events and the results from Chapter 4 show that care-givers were able to increase the provisioning effort (increasing provisioning to one fledgling without decreasing feeding levels to other offspring). Conducting similar experiments to Chapter 4 in a drought year, when food is not so readily available, may yield very different results. Under harsh environmental conditions adults may not be as flexible, and care-givers may be unable to maintain provisioning levels to control fledglings when an experimental chick's begging is increased. Thus, in times of food stress, I predict that fledgling begging would be more likely to escalate when their siblings' begging increases, in order to maintain the level of care they receive. In situations where food becomes a limiting factor, scramble competition is more likely as offspring seek to gain access to their share of finite resources (Royle et al. 2004; Grodzinski & Johnstone 2012). I also predict that group size may have a stronger effect on begging dynamics, as smaller groups may be less able to cope with increased demand under drought conditions (Ridley & Raihani 2007a). If group size became an important factor, it would help to add evidence in support of the theory that cooperation is selected for in unpredictable environments (Rubenstein & Lovette 2007; Rubenstein 2011).

The cost of begging is crucial to predictions regarding begging behaviour (Grafen 1990; Godfray 1991; Johnstone 1996b; Parker et al. 2002). The costs of begging have been investigated in nestlings: metabolic (Leech & Leonard 1996; Bachman & Chappell 1998)), predation (Haskell 1994; Haskell 1999; McDonald et al. 2009), growth (Kilner 2001) and

immunological (Moreno-Rueda 2010). However, the cost of begging in mobile young remains unexamined. The cost of begging for mobile offspring is likely to be different for two reasons: firstly, Predation risk may be lower for fledglings, as offspring are no longer a fixed source of noise in the environment (Leonard & Horn 2006), the location of which predators can learn. Secondly, avian offspring typically only become mobile once they have become relatively well developed, suggesting that the costs of signal production may be reduced. Additional work investigating the costs of begging in fledgling pied babblers would help to shed light on this begging system. Due to the nature of the pied babbler study population, habituated wild free-living birds, metabolic costs would be difficult to measure. Predation costs could be measured using a series of experiments playing back begging calls, combined with cameras to record the latency until predator arrival. A few simple questions could be asked: do crescendo begs carry a higher predation cost than repeat begs? What is the predation cost of an increased begging rate? Do begging calls from hungrier fledglings carry higher predation costs? Understanding these costs would help in modelling the more complex begging behaviour of mobile offspring.

References

Acerbi, A., Marocco, D., & Nolfi, S. 2007. Social facilitation on the development of foraging behaviors in a population of autonomous robots. *Advances in Artificial Life*, **4648**, 625–634.

Addessi, E., Galloway, A. T., Visalberghi, E., & Birch, L. L. 2005. Specific social influences on the acceptance of novel foods in 2-5-year-old children. *Appetite*, **45**, 264–271.

Allen, T., & Clarke, J. 2005. Social learning of food preferences by white-tailed ptarmigan chicks. *Animal Behaviour*, **70**, 305–310.

Alonso-Alvarez, C., Bertrand, S., Devevey, G., Prost, J., Faivre, B., Chastel, O., & Sorci, G. 2006. An experimental manipulation of life-history trajectories and resistance to oxidative stress. *Evolution*, **60**, 1913–1924.

Alonso-Alvarez, C., & Velando, A. 2012. Benefits and costs of parental care. In: *The Evolution of Parental Care*, (Ed. by N. J. Royle, P. T. Smiseth, & M. Kölliker), pp. 40–61. Oxford University Press.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **3**, 227–267.

Anderson, M. G., Brunton, D. H., & Hauber, M. E. 2010. Reliable information content and ontogenetic shift in begging calls of grey warbler nestlings. *Ethology*, **116**, 357–365.

Anderson, D. R., Burnham, K. P., & Thompson, W. L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.

Bachman, G. C., & Chappell, M. A. 1998. The energetic cost of begging behaviour in nestling house wrens. *Animal Behaviour*, **55**, 1607–1618.

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., & Werner, N. 2001. Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, **50**, 134–140.

Beecher, M. D., & Burt, J. M. 2004. The role of social interaction in bird song learning. *Current Directions in Psychological Science*, **13**, 224–228.

Bell, M. B. V. 2007. Cooperative begging in banded mongoose pups. *Current Biology*, **17**, 717–721.

Bell, M. B. V. 2008a. Strategic adjustment of begging effort by banded mongoose pups. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1313–1319.

Bell, M. B. V. 2008b. Receiver identity modifies begging intensity independent of need in banded mongoose (*Mungos mungo*) pups. *Behavioral Ecology*, **19**, 1087–1094.

Bell, M. B. V, Radford, A. N., Rose, R., Wade, H. M., & Ridley, A. R. 2009. The value of constant surveillance in a risky environment. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2997–3005.

Bell, M. B. V, Radford, A. N., Smith, R. A., Thompson, A. M., & Ridley, A. R. 2010. Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3223–3228.

Bereczkei, T., Gyuris, P., & Weisfeld, G. E. 2004. Sexual imprinting in human mate choice. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1129–1134.

Berg, K. S., Beissinger, S. R., & Bradbury, J. W. 2013. Factors shaping the ontogeny of vocal signals in a wild parrot. *Journal of Experimental Biology*, **216**, 338–345.

Bird Life International. 2013. Species factsheet: *Turdoides bicolor*. *IUCN Red List for birds*,

den Boer, S. P. A., & Duchateau, M. J. H. M. 2006. A larval hunger signal in the bumblebee *Bombus terrestris*. *Insectes Sociaux*, **53**, 369–373.

Briskie, J. V., Martin, P. R., & Martin, T. E. 1999. Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 2153–2159.

Briskie, J. V, Naugler, C. T., & Leech, S. M. 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proceedings of the Royal Society B: Biological Sciences*, **258**, 73–78.

Brittan-Powell, E. F., Dooling, R. J., & Farabaugh, S. M. 1997. Vocal development in budgerigars (*Melopsittacus undulatus*): contact calls. *Journal of Comparative Psychology*, **111**, 226–241.

Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R., & McIlrath, G. M. 2001. Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, **12**, 590–599.

Brown, J. L. 1987. *Helping and Communal Breeding in Birds.* Princeton, New Jersey: Princeton University Press.

Brown, J. L., Dow, D. D., Brown, E. R., & Brown, S. D. 1978. Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behavioral Ecology and Sociobiology*, **4**, 43–59.

Bulmer, E., Celis, P., & Gil, D. 2008. Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). *Behavioral Ecology*, **19**, 279–284.

Burnham, K. P., & Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach.* New York: Springer.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, **65**, 23–35.

Butchart, S. H. M., Kilner, R. M., Fuisz, T., & Davies, N. B. 2003. Differences in the nestling begging calls of hosts and host-races of the common cuckoo, *Cuculus canorus*. *Animal Behaviour*, **65**, 345–354.

Cant, M. A. 2012. Cooperative breeding systems. In: *The Evolution of Parental Care*, (Ed. by N. J. Royle, P. T. Smiseth, & M. Kölliker), pp. 206–225. Oxford University Press.

Caro, T. M., & Hauser, M. D. 1992. Is there teaching in nonhuman animals? *Quarterly Review of Biology*, **67**, 151–174.

Charrier, I., Mathevon, N., & Jouventin, P. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, **205**, 603–612.

Charrier, I., Mathevon, N., Jouventin, P., & Aubin, T. 2001. Acoustic communication in a black-headed gull colony: how do chicks identify their parents? *Ethology*, **107**, 961–974.

Child, M. F., Flower, T. P., & Ridley, A. R. 2012. Investigating a link between bill morphology, foraging ecology and kleptoparasitic behaviour in the fork-tailed drongo. *Animal Behaviour*, **84**, 1013–1022.

Clemmons, J., & Howitz, J. L. 1990. Development of early vocalizations and the chick-a-dee call in the black-capped chickadee, *Parus atricapillus*. *Ethology*, **86**, 203–223.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, **296**, 69–72.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N., McIlrath, G. M., White, S., & Cameron, E. Z. 2001. Effects of helpers on juvenile development and survival in meerkats. *Science*, **293**, 2446–9.

Cockburn, A. 1991. *An Introduction to Evolutionary Ecology.* Oxford, UK: Blackwell Scientific Publications.

Cornwallis, C. K., West, S. A., Davis, K. E., & Griffin, A. S. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature*, **466**, 969–972.

Cotton, P. A., Kacelnik, A., & Wright, J. 1996. Chick begging as a signal: are nestlings honest? *Behavioral Ecology*, **7**, 178–182.

Cotton, P. A., Wright, J., & Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist*, **153**, 412–420.

Crockford, C., & Boesch, C. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, **66**, 115–125.

Cumming, G. S., & Bernard, R. T. F. 1997. Rainfall, food abundance and timing of parturition in African bats. *Oecologia*, **111**, 309–317.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, **20**, 187–93.

Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487–91.

Darwin, C. 1859. *On The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* London: John Murray.

Davies, N. B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour*, **59**, 280–295.

Davies, N. B., Butchart, S. H. M., Burke, T. A., Chaline, N., & Stewart, I. R. K. 2003. Reed warblers guard against cuckoos and cuckoldry. *Animal Behaviour*, **65**, 285–295.

Davies, N. B., & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.

Davies, N. B., Krebs, J. R., & West, S. A. 2012. Sex allocation. In: *An Introduction to Behavioural Ecology*, Fourth edn. (Ed. by N. B. Davies, J. R. Krebs, & S. A. West), pp. 282–306. Wiley-Blackwell.

Davies, N. B., Madden, J. R., & Butchart, S. H. M. 2004. Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 2297–2304.

Dittus, W. J. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour*, **32**, 471–477.

Draganoiu, T. I., Nagle, L., Musseau, R., & Kreutzer, M. 2006. In a songbird, the black redstart, parents use acoustic cues to discriminate between their different fledglings. *Animal Behaviour*, **71**, 1039–1046.

Dreiss, A., Lahlah, N., & Roulin, A. 2010. How siblings adjust sib–sib communication and begging signals to each other. *Animal Behaviour*, **80**, 1049–1055.

Dukas, R. 2005. Experience improves courtship in male fruit flies. *Animal Behaviour*, **69**, 1203–1209.

Dukas, R., & Visscher, P. K. 1994. Lifetime learning by foraging honey bees. *Animal Behaviour*, **48**, 1007–1012.

Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, **34**, 169–174.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology: An Evolutionary Approach*, Third edn. (Ed. by J. R. Krebs & N. B. Davies), pp. 301–337. Blackwell Scientific Publications.

English, S., Kunc, H. P., Madden, J. R., & Clutton-Brock, T. H. 2008. Sex differences in responsiveness to begging in a cooperative mammal. *Biology Letters*, **4**, 334–7.

Espmark, Y., & Langvatn, R. 1985. Development and habituation of cardiac and behavioral responses in young red deer calves (*Cervus elaphus*) exposed to alarm stimuli. *American Society of Mammalogists*, **66**, 702–711.

Ey, E., & Fischer, J. 2009. The "Acoustic adaptiation hypothesis" - A review of the evidence from birds, anurans and mammals. *Bioacoustics*, **19**, 21–48.

Fairhurst, E. N., Horn, A. G., & Leonard, M. L. *INPRESS*. Nest acoustics and begging call structure in nestling tree swallows. *Animal Behaviour*

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**, 1213–1222.

Flores, E. R., Provenza, F. D., & Balph, D. F. 1989. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. *Applied Animal Behaviour Science*, **23**, 271–278.

Franklin, E. L., & Franks, N. R. 2012. Individual and social learning in tandem-running recruitment by ants. *Animal Behaviour*, **84**, 361–368.

Franks, N. R., & Richardson, T. 2006. Teaching in tandem-running ants. *Nature*, **439**, 153.

Galef, B. G., & Giraldeau, L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3–15.

Gebhardt-Henrich, S., & Richner, H. 1998. Causes of growth variation and its consequences for fitness. In: *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*, (Ed. by M. J. Starck & R. E. Ricklefs), pp. 324–339. Oxford University Press.

Gerlach, N. M., McGlothlin, J. W., Parker, P. G., & Ketterson, E. D. 2012. Promiscuous mating produces offspring with higher lifetime fitness. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 860–866.

Ghalambor, C. K., & Martin, T. E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, **292**, 494–497.

Gilchrist, J. S. 2004. Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behavioral Ecology*, **15**, 952–960.

Gilchrist, J. S. 2006. Reproductive success in a low skew, communal breeding mammal: the banded mongoose, *Mungos mungo*. *Behavioral Ecology and Sociobiology*, **60**, 854–863.

Giraldeau, L.-A. 1984. Group foraging: the skill pool effect and frequency-dependent learning. *American Naturalist*, **124**, 72–79.

Giraldeau, L.-A., & Templeton, J. J. 1991. Food scrounging and diffusion of foraging skills in pigeons, *Columba livia*: the importance of tutor and observer rewards. *Ethology*, **72**, 63–72.

Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature*, **352**, 328–330.

Godfray, H. C. J. 1995. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *American Naturalist*, **146**, 1–24.

Godfray, H. C. J., & Johnstone, R. A. 2000. Begging and bleating: the evolution of parent-offspring signalling. *Proceedings of the Royal Society B: Biological Sciences*, **355**, 1581–1591.

Golabek, K. A., & Radford, A. N. 2013. Chorus-call classification in the southern pied babbler: multiple call types given in overlapping contexts. *Behaviour*,

Golabek, K. A., Ridley, A. R., & Radford, A. N. 2012. Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour*, **83**, 613–619.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. In: *Reproductive Success*, (Ed. by T. H. Clutton-Brock), pp. 454–471. Chicago, IL: University of Chicago Press.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Greig, E. I., Taft, B. N., & Pruett-Jones, S. 2012. Sons learn songs from their social fathers in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3154–3160.

Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., O'Riain, J., & Clutton-Brock, T. H. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology*, **14**, 472–480.

Griffiths, R., Double, M. C., Orr, K., & Dawson, J. G. 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

Grodzinski, U., Erev, I., & Lotem, A. 2007. Can hungry nestlings be trained to reduce their begging? *Behavioral Ecology*, **19**, 116–125.

Grodzinski, U., & Johnstone, R. A. 2012. Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 109–115.

Grodzinski, U., & Lotem, A. 2007. The adaptive value of parental responsiveness to nestling begging. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2449–2456.

Grovenburg, T. W., Monteith, K. L., Klaver, R. W., & Jenks, J. A. 2012. Predator evasion by white-tailed deer fawns. *Animal Behaviour*, **84**, 59–65.

Haff, T. M., & Magrath, R. D. 2010. Vulnerable but not helpless: nestlings are fine-tuned to cues of approaching danger. *Animal Behaviour*, **79**, 487–496.

Hamilton, W. D. 1963. The evolution of altruistic behavior. *American Naturalist*, **97**, 354–356.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, **7**, 17–52.

Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proceedings of the Royal Society B: Biological Sciences*, **257**, 161–164.

Haskell, D. G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Animal Behaviour*, **57**, 893–901.

Hatchwell, B. J. 1999. Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist*, **154**, 205–219.

Hauber, M. E., & Ramsey, C. K. 2003. Honesty in host-parasite communication signals: the case for begging by fledgling brown-headed cowbirds *Molothrus ater*. *Journal of Avian Biology*, **34**, 339–344.

Heinsohn, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, **137**, 864–881.

Hinde, C. A. 2006. Negotiation over offspring care?-a positive response to partner-provisioning rate in great tits. *Behavioral Ecology*, **17**, 6–12.

Hinde, C. A., Buchanan, K. L., & Kilner, R. M. 2009. Prenatal environmental effects match offspring begging to parental provisioning. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2787–2794.

Hinde, C. A., Johnstone, R. A., & Kilner, R. M. 2010. Parent-offspring conflict and coadaptation. *Science*, **327**, 1373–1376.

Hinde, C. A., & Kilner, R. M. 2007. Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 53–60.

Hockey, P. A. R., Dean, W. R. J., & Ryan, P. G. Eds. 2005. *Roberts Birds of Southern Africa.* 7th edn. Cape Town: Trustees of the John Voelcker Bird Book Fund.

Hodge, S. J. 2005. Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2479–2484.

Hodge, S. J., Bell, M. B. V, Mwanguhya, F., Kyabulima, S., Waldick, R. C., & Russell, A. F. 2009. Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behavioral Ecology*, **20**, 729–735.

Hodge, S. J., Flower, T. P., & Clutton-Brock, T. H. 2007. Offspring competition and helper associations in cooperative meerkats. *Animal Behaviour*, **74**, 957–964.

Hollén, L. I., Bell, M. B. V, & Radford, A. N. 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, **18**, 576–579.

Hollén, L. I., Bell, M. B. V, Wade, H. M., Rose, R., Russell, A., Niven, F., Ridley, A. R., & Radford, A. N. 2011. Ecological conditions influence sentinel decisions. *Animal Behaviour*, **82**, 1435–1441.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology*, **67**, 737–748.

Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., & Laland, K. N. 2008. Lessons from animal teaching. *Trends in Ecology & Evolution*, **23**, 486–93.

Hudson, R., & Trillmich, F. 2007. Sibling competition and cooperation in mammals: challenges, developments and prospects. *Behavioral Ecology and Sociobiology*, **62**, 299–307.

Hurvich, C. M., & Tsai, C.-L. 1989. Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Jacob, S., Rieucau, G., & Heeb, P. 2011. Multimodal begging signals reflect independent indices of nestling condition in European starlings. *Behavioral Ecology*, **22**, 1249–1255.

Jakob, E. M., Marshall, S. D., & Uetz, G. W. 1996. Estimating Fitness: A Comparison of Body Condition Indices indices. *Oikos*, **77**, 61–67.

Johnstone, R. A. 1996a. Multiple displays in animal communication: "backup signals" and "multiple messages". *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 329–338.

Johnstone, R. A. 1996b. Begging signals and parent-offspring conflict: do parents always win? *Proceedings of the Royal Society B: Biological Sciences*, **263**, 1677–1681.

Johnstone, R. A. 2004. Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist*, **163**, 388–406.

Johnstone, R. A., & Grafen, A. 1992. The continuous Sir Philip Sidney Game: a simple model of biological signalling. *Journal of Theoretical Biology*, **156**, 215–234.

Johnstone, R. A., & Grafen, A. 1993. Dishonesty and the handicap principle. *Animal Behaviour*, **46**, 759–764.

Johnstone, R. A., & Kilner, R. M. 2011. New labels for old whines. *Behavioral Ecology*, **22**, 918–919.

Johnstone, R. A., & Roulin, A. 2003. Sibling negotiation. *Behavioral Ecology*, **14**, 780–786.

Jouventin, P., Aubin, T., & Lengagne, T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour*, **57**, 1175–1183.

Jurisevic, M. A. 1999. Structural change of begging vocalisations and vocal repertoires in two hand-raised Australian passerines, the little raven *Corvus mellor* and white-winged chough *Corcorax melanorhamphos*. *Emu*, **99**, 1–8.

Jurisevic, M. A. 2003. Convergent characteristics of begging vocalisations in Australian birds. *Lundiana*, **4**, 25–33.

Kacelnik, A., Cotton, P. A., Stirling, L., & Wright, J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proceedings of the Royal Society B: Biological Sciences*, **259**, 259–263.

Kahn, A. T., Livingston, J. D., & Jennions, M. D. 2012. Do females preferentially associate with males given a better start in life ? *Biology Letters*, **8**, 362–364.

Kaptein, N., Billen, J., & Gobin, B. 2005. Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. *Animal Behaviour*, **69**, 293–299.

Kedar, H., Rodríguez-Gironés, M. A., Yedvab, S., Winkler, D. W., & Lotem, A. 2000. Experimental evidence for offspring learning in parent-offspring communication. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 1723–1727.

Kilner, R. M. 1995. When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society B: Biological Sciences*, **260**, 343–348.

Kilner, R. M. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 963–968.

Kilner, R. M. 2001. A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences*, **98**, 11394–11398.

Kilner, R. M. 2002a. The evolution of complex begging displays. In: *The Evolution of Begging: Competition, Cooperation and Communication*, (Ed. by J. Wright & M. L. Leonard), pp. 87–106. Kluwer Academic Publishers.

Kilner, R. M. 2002b. Sex differences in canary (*Serinus canaria*) provisioning rules. *Behavioral Ecology and Sociobiology*, **52**, 400–407.

Kilner, R. M., & Davies, N. B. 1999. How selfish is a cuckoo chick? *Animal Behaviour*, **58**, 797–808.

Kilner, R. M., & Hinde, C. A. 2008. Information warfare and parent-offspring conflict. *Advances in the Study of Behavior*, **38**, 283–336.

Kilner, R. M., & Hinde, C. A. 2012. Parent-offspring conflict. In: *The Evolution of Parental Care*, (Ed. by N. J. Royle, P. T. Smiseth, & M. Kölliker), pp. 119–132. Oxford, UK: Oxford University Press.

Kilner, R. M., & Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology & Evolution*, **12**, 11–15.

Kilner, R. M., Madden, J. R., & Hauber, M. E. 2004. Brood parasitic cowbird nestlings use host young to procure resources. *Science*, **305**, 877–879.

Kilner, R. M., Noble, D. G., & Davies, N. B. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.

Kleindorfer, S., Hoi, H., & Fessl, B. 1996. Alarm calls and chick reactions in the moustached warbler, *Acrocephalus melanopogon*. *Animal Behaviour*, **51**, 1199–1206.

Knouft, J. H., Page, L. M., & Plewa, M. J. 2003. Antimicrobial egg cleaning by the fringed darter (Perciformes: Percidae: *Etheostoma crossopterum*): implications of a novel component of parental care in fishes. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2405–2411.

Kodric-Brown, A., & Nicoletto, P. F. 2001. Age and experience affect female choice in the guppy (*Poecilia reticulata*). *American Naturalist*, **157**, 316–323.

Koenig, W. D. 1981. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *American Naturalist*, **117**, 421–443.

Kölliker, M. 2003. Estimating mechanisms and equilibria for offspring begging and parental provisioning. *Proceedings of the Royal Society B: Biological Sciences*, **270 Suppl** , S110–S113.

Kölliker, M., Brinkhof, M. W., Heeb, P., Fitze, P. S., & Richner, H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 2127–2132.

Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E., & Guinness, F. E. 1999. Early determinants of lifetime reporductive success differ detween the sexes in red deer. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1655–1661.

Kunc, H. P., Madden, J. R., & Manser, M. B. 2007. Begging signals in a mobile feeding system: the evolution of different call types. *American Naturalist*, **170**, 617–624.

Laland, K. N., & Plotkin, H. C. 1992. Further experimental analysis of the social learning and transmission of foraging information amongst Norway rats. *Behavioural Processes*, **27**, 53–64.

Langen, T. A. 1996a. Social learning of a novel foraging skill by white throated magie jays (*Calocitta formosa*, Corvidae): a field experiment. *Ethology*, **102**, 157–166.

Langen, T. A. 1996b. Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*. *Animal Behaviour*, **51**, 575–588.

Langen, T. A. 2000. Prolonged offspring dependence and cooperative breeding in birds. *Behavioral Ecology*, **11**, 367–377.

Langen, T. A., & Vehrencamp, S. L. 1999. How white-throated magpie-jay helpers contribute during breeding. *Auk*, **116**, 131–140.

Lee, P. C., Bussière, L. F., Webber, C. E., Poole, J. H., & Moss, C. J. 2013. Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (*Loxodonta africana*). *Biology Letters*, **9**, 20130011.

Leech, S. M., & Leonard, M. L. 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? *Proceedings of the Royal Society B: Biological Sciences*, **263**, 983–987.

Leech, S. M., & Leonard, M. L. 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology*, **8**, 644–646.

Leonard, M. L., & Horn, A. G. 1998. Need and nestmates affect begging in tree swallows. *Behavioral Ecology and Sociobiology*, **42**, 431–436.

Leonard, M. L., & Horn, A. G. 2001a. Begging in the absence of parents by nestling tree swallows. *Behavioral Ecology*, **12**, 501–505.

Leonard, M. L., & Horn, A. G. 2001b. Acoustic signalling of hunger and thermal state by nestling tree swallows. *Animal Behaviour*, **61**, 87–93.

Leonard, M. L., & Horn, A. G. 2006. Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). *Ethology*, **112**, 1020–1026.

Lima, S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos*, **53**, 3–11.

Lima, S. L., & Dill, L. M. 1990. Beahvioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343–348.

Lonsdorf, E. V. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, **70**, 673–683.

De Luca, D. W., & Ginsberg, J. R. 2001. Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system? *Animal Behaviour*, **61**, 17–30.

Lukas, D., & Clutton-Brock, T. 2012. Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2151–2156.

Lummaa, V., Vuorisalo, T., Barr, R. G., & Lehtonen, L. 1998. Why cry? Adaptive significance of intensive crying in human infants. *Evolution and Human Behavior*, **19**, 193–202.

MacGregor, N. A., & Cockburn, A. 2002. Sex differences in parental response to begging nestlings in superb fairy-wrens. *Animal Behaviour*, **63**, 923–932.

Mackney, P. A., & Hughes, R. N. 1995. Foraging behaviour and memory window in sticklebacks. *Behaviour*, **132**, 1241–1253.

MacNair, M. R., & Parker, G. A. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. *Animal Behaviour*, **27**, 1202–1209.

Madden, J. R., & Davies, N. B. 2006. A host-race difference in begging calls of nestling cuckoos *Cuculus canorus* develops through experience and increases host provisioning. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2343–2351.

Madden, J. R., Kilner, R. M., & Davies, N. B. 2005. Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. *Animal Behaviour*, **70**, 619–627.

Madden, J. R., Kunc, H.-J. P., English, S., & Clutton-Brock, T. H. 2009a. Why do meerkat pups stop begging? *Animal Behaviour*, **78**, 85–89.

Madden, J. R., Kunc, H.-J. P., English, S., Manser, M. B., & Clutton-Brock, T. H. 2009b. Calling in the gap: competition or cooperation in littermates' begging behaviour? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1255–1262.

Madden, J. R., Kunc, H.-J. P., English, S., Manser, M. B., & Clutton-Brock, T. H. 2009c. Do meerkat (*Suricata suricatta*) pups exhibit strategic begging behaviour and so exploit adults that feed at relatively high rates? *Behavioral Ecology and Sociobiology*, **63**, 1259–1268.

Magrath, R. D., Haff, T. M., Horn, A. G., & Leonard, M. L. 2010. Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. *Advances in the Study of Behavior*, **41**, 187–253.

Magrath, R. D., & Heinsohn, R. G. 2000. Reproductive skew in birds: models, problems and prospects. *Journal of Avian Biology*, **31**, 247–258.

Magrath, R. D., Pitcher, B., & Dalziell, A. H. 2007. How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator's footsteps. *Animal Behaviour*, **74**, 1117–1129.

Magrath, R. D., Platzen, D., & Kondo, J. 2006. From nestling calls to fledgling silence: adaptive timing of change in response to aerial alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2335–41.

Manser, M. B. 2001a. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, 2315–2324.

Manser, M. B. 2001b. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2315–24.

Manser, M. B., & Avey, G. 2000. The effect of pup vocalisations on food allocation in a cooperative mammal, the meerkat (*Suricata suricatta*). *Behavioral Ecology and Sociobiology*, **48**, 429–437.

Manser, M. B., Madden, J. R., Kunc, H.-J. P., English, S., & Clutton-Brock, T. 2008. Signals of need in a cooperatively breeding mammal with mobile offspring. *Animal Behaviour*, **76**, 1805–1813.

Margulis, S. W., Nabong, M., Alaks, G., Walsh, A., & Lacy, R. C. 2005. Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Animal Behaviour*, **69**, 627–634.

Marques, P. A. M., Leonard, M. L., Horn, A. G., & Contasti, A. 2011. How nestling tree swallows (*Tachycineta bicolor*) integrate their responses to hunger and signalling by nestmates. *Ethology*, **117**, 163–170.

Marques, P. A. M., Vicente, L., & Márquez, R. 2009. Nestling begging call structure and bout variation honestly signal need but not condition in Spanish sparrows. *Zoological Studies*, **48**, 587–595.

Martin, P., & Bateson, P. 2007. Recording Methods. In: *Measuring Behaviour: An Introductory Guide*, 3rd edn. pp. 48–61. Cambridge University Press.

Mas, F., Haynes, K. F., & Kölliker, M. 2009. A chemical signal of offspring quality affects maternal care in a social insect. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2847–2853.

Mas, F., & Kölliker, M. 2008. Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. *Animal Behaviour*, **76**, 1121–1131.

Mathevon, N., & Charrier, I. 2004. Parent-offspring conflict and the coordination of siblings in gulls. *Proceedings of the Royal Society B: Biological Sciences*, **271**, S145–S147.

Mauck, R. a, & Grubb Jr, T. C. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour*, **49**, 999–1008.

McCarty, J. P. 1996. The energetic cost of begging in nestling passerines. *Auk*, **113**, 178–188.

McDonald, P. G., Wilson, D. R., & Evans, C. S. 2009. Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. *Behavioral Ecology*, **20**, 821–829.

McGowan, K. J., & Woolfenden, G. E. 1990. Contributions to fledgling feeding in the Florida scrub jay. *Journal of Animal Ecology*, **59**, 691–707.

Meade, J., Nam, K.-B., Beckerman, A. P., & Hatchwell, B. J. 2010. Consequences of "load-lightening" for future indirect fitness gains by helpers in a cooperatively breeding bird. *Journal of Animal Ecology*, **79**, 529–537.

Midford, P. E., Hailman, J. P., & Woolfenden, G. E. 2000. Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Animal Behaviour*, **59**, 1199–1207.

Mock, D. W. 1987. Siblicide, parent-offspring conflict and unequal parental investment by egrets and herons. *Behavioral Ecology*, **20**, 247–256.

Mock, D. W., Dugas, M. B., & Strickler, S. A. 2011. Honest begging: expanding from Signal of Need. *Behavioral Ecology*, **22**, 909–917.

Mock, D. W., & Forbes, L. S. 1992. Parent-offspring conflict: a case of arrested development. *Nature*, **7**, 409–413.

Mock, D. W., & Parker, G. A. 1998. Siblicide, family conflict and the evolutionary limits of selfishness. *Animal Behaviour*, **56**, 1–10.

Møller, A. P., & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, **32**, 167–176.

Monaghan, P., & Nager, R. G. 1997. Why don't birds lay more eggs? *Trends in Ecology & Evolution*, **12**, 270–274.

Monk, D. S., Koenig, W. D., & Koenig, W. R. 1997. Individual, brood, and sex variation in begging calls of western bluebirds. *The Wilson Bulletin*, **109**, 328–332.

Moreno-Rueda, G. 2010. An immunological cost of begging in house sparrow nestlings. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2083–2088.

Moscovice, L. R., & Snowdon, C. T. 2006. The role of social context and individual experience in novel task acquisition in cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, **71**, 933–943.

Muller, R. E., & Smith, D. G. 1978. Parent-offspring interactions in zebra finches. *Auk*, **95**, 485–495.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology*, **31**, 319–328.

Mundry, R., & Sommer, C. 2007. Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behaviour*, **74**, 965–976.

Nelson-Flower, M. J. 2009. Kinship and its consequences in the cooperatively breeding Southern Pied Babbler *Turdoides bicolor*. University of Cape Town.

Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C., Raihani, N. J., Du Plessis, M. A., & Ridley, A. R. 2011. Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behavioral Ecology*, **22**, 559–565.

Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C., & Ridley, A. R. 2012. Inbreeding avoidance mechanisms: dispersal dynamics in cooperatively breeding southern pied babblers. *Journal of Animal Ecology*, **81**, 876–883.

Neuenschwander, S., Brinkhof, M. W. G., Kölliker, M., & Richner, H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology*, **14**, 457–462.

Nicol, C. 2006. How animals learn from each other. *Applied Animal Behaviour Science*, **100**, 58–63.

Nonacs, P., & Dill, L. M. 1990. Mortality risk vs food quality trade-offs in a common currency: ant patch references. *Ecology*, **71**, 1886–1892.

Nur, N. 1988. The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution*, **42**, 351–362.

O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Animal Behaviour*, **26**, 79–96.

Page, B., Goldsworthy, S. D., & Hindell, M. A. 2002. Individual vocal traits of mother and pup fur seals. *Bioacoustics*, **13**, 121–143.

Parker, G. A., Mock, D. W., & Lamey, T. C. 1989. How selfish should stronger sibs be? *American Naturalist*, **133**, 846–868.

Parker, G. A., Royle, N. J., & Hartley, I. R. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology*, **5**, 206–215.

Platzen, D., & Magrath, R. D. 2004. Parental alarm calls suppress nestling vocalization. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1271–1276.

Platzen, D., & Magrath, R. D. 2005. Adaptive differences in response to two types of parental alarm call in altricial nestlings. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1101–1106.

van de Pol, M., Bruinzeel, L. W., Heg, D., van der Jeugd, H. P., & Verhulst, S. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **75**, 616–626.

Price, K. 1996. Begging as competition for food in yellow-headed blackbirds. *Auk*, **113**, 963–967.

Price, K., Harvey, H., & Ydenberg, R. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour*, **51**, 421–435.

Price, K., & Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behavioral Ecology*, **37**, 201–208.

Quinn, G. P., & Keough, M. J. 2002. Multivariate analysis of variance and discriminant analysis. In: *Experimental Design and Data Analysis for Biologists*, pp. 425–441. Cambridge, UK: Cambridge University Press.

Radford, A. N., & Ridley, A. R. 2006. Recruitment calling: a novel form of extended parental care in an altricial species. *Current Biology*, **16**, 1700–1704.

Raihani, N. J. 2008. Cooperation and conflict in pied babblers. University of Cambridge.

Raihani, N. J., Nelson-Flower, M. J., Golabek, K. A., & Ridley, A. R. 2010. Routes to breeding in cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, **41**, 681–686.

Raihani, N. J., & Ridley, A. R. 2007a. Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers. *Animal Behaviour*, **74**, 1303–1309.

Raihani, N. J., & Ridley, A. R. 2007b. Variable fledging age according to group size: trade-offs in a cooperatively breeding bird. *Biology Letters*, **3**, 624–627.

Raihani, N. J., & Ridley, A. R. 2008a. Experimental evidence for teaching in wild pied babblers. *Animal Behaviour*, **75**, 3–11.

Raihani, N. J., & Ridley, A. R. 2008b. Parental aggression against dependent young results in task partitioning in a cooperatively breeding bird. *Biology Letters*, **4**, 23–26.

Raihani, N. J., Ridley, A. R., Browning, L. E., Nelson-Flower, M. J., & Knowles, S. 2008. Juvenile female aggression in cooperatively breeding pied babblers: causes and contexts. *Ethology*, **114**, 452–458.

Rauter, C. M., & Moore, A. J. 1999. Do honest signalling models of offspring solicitation apply to insects? *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1691–1696.

Reader, S. M., Kendal, J. R., & Laland, K. N. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, **66**, 729–739.

Reader, S. M., & Laland, K. N. 2000. Diffusion of foraging innovations in the guppy. *Animal Behaviour*, **60**, 175–180.

Redondo, T., & Carranza, J. 1989. Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behavioral Ecology and Sociobiology*, **25**, 369–378.

Redondo, T., & Castro, F. 1992. Signalling of nutritional need by magpie nestlings. *Ethology*, **92**, 193–204.

Redondo, T., & Exposito, F. 1990. Structural variations in the begging calls of nestling magpies *Pica pica* and their role in the development of adult voice. *Ethology*, **84**, 307–318.

Rendell, L., & Whitehead, H. 2001. Culture in whales and dolphins. *The Behavioral and Brain Sciences*, **24**, 309–324.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Ridley, A. R. 2007. Factors affecting offspring survival and development in a cooperative bird: social, maternal and environmental effects. *Journal of Animal Ecology*, **76**, 750–760.

Ridley, A. R., & Child, M. F. 2009. Specific targeting of host individuals by a kleptoparasitic bird. *Behavioral Ecology and Sociobiology*, **63**, 1119–1126.

Ridley, A. R., & van den Heuvel, I. M. 2012. Is there a difference in reproductive performance between cooperative and non-cooperative species? A southern African comparison. *Behaviour*, **8**, 821–848.

Ridley, A. R., & Huyvaert, K. P. 2007. Sex-biased preferential care in the cooperatively breeding Arabian babbler. *Journal of Evolutionary Biology*, **20**, 1271–1276.

Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. 2013. Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, **85**, 137–142.

Ridley, A. R., & Raihani, N. J. 2007a. Variable postfledging care in a cooperative bird: causes and consequences. *Behavioral Ecology*, **18**, 994–1000.

Ridley, A. R., & Raihani, N. J. 2007b. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, **18**, 324–330.

Ridley, A. R., & Raihani, N. J. 2008. Task partitioning increases reproductive output in a cooperative bird. *Behavioral Ecology*, **19**, 1136–1142.

Ridley, A. R., Raihani, N. J., & Bell, M. B. V. 2010. Experimental evidence that sentinel behaviour is affected by risk. *Animal Behaviour*, **6**, 445–448.

Ridley, A. R., Raihani, N. J., & Nelson-Flower, M. J. 2008. The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, **39**, 389–392.

Ridley, A. R., & Thompson, A. M. 2011. Heterospecific egg destruction by wattled starlings and the impact on pied babbler reproductive success. *Ostrich*, **82**, 201–205.

Riou, S., Chastel, O., & Hamer, K. C. 2012. Parent-offspring conflict during the transition to independence in a pelagic seabird. *Behavioral Ecology*, **23**, 1102–1107.

Rodríguez-Gironés, M. A. 1999. Sibling competition stabilizes signalling resolution models of parent-offspring conflict. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 2399–2402.

Rodríguez-Gironés, M. A., Enquist, M., & Lachmann, M. 2001. Role of begging and sibling competition in foraging strategies of nestlings. *Animal Behaviour*, **61**, 733–745.

Romano, A., Caprioli, M., Boncoraglio, G., Saino, N., & Rubolini, D. 2012. With a little help from my kin: barn swallow nestlings modulate solicitation of parental care according to nestmates' need. *Journal of Evolutionary Biology*, **25**, 1703–1710.

Roulin, A. 2002. The sibling negotiation hypothesis. In: *The Evolution of Begging: Competition, Cooperation and Communication*, (Ed. by J. Wright & M. L. Leonard), pp. 107–126. Kluwer Academic Publishers.

Roulin, A., Kölliker, M., & Richner, H. 2000. Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 459–463.

Rovero, F., Hughes, R. N., & Chelazzi, G. 1999. Effect of experience on predatory behaviour of dogwhelks. *Animal Behaviour*, **57**, 1241–1249.

Rowe, C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, **58**, 921–931.

Royle, N. J., Hartley, I. R., & Parker, G. A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*, **17**, 434–440.

Royle, N. J., Hartley, I. R., & Parker, G. A. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. *Population Ecology*, **46**, 231–241.

Rubenstein, D. R. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences*, **108**, 10816–10822.

Rubenstein, D. R., & Lovette, I. J. 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology*, **17**, 1414–1419.

Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B., & Kilner, R. M. 2007a. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*, **317**, 941–944.

Russell, A. F., Langmore, N. E., Gardner, J. L., & Kilner, R. M. 2008. Maternal investment tactics in superb fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 29–36.

Russell, E. M., Yom-Tov, Y., & Geffen, E. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology*, **15**, 831–838.

Russell, A. F., Young, A. J., Spong, G., Jordan, N. R., & Clutton-Brock, T. H. 2007b. Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 513–520.

Rydén, O., & Bengtsson, H. 1980. Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. *Zeitschrift für Tierpsychologie*, **53**, 201–224.

Sacchi, R., Saino, N., & Galeotti, P. 2002. Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behavioral Ecology*, **13**, 268–273.

Saino, N., Galeotti, P., Sacchi, R., Boncoraglio, G., Martinelli, R., & Møller, A. P. 2003. Sex differences in begging vocalizations of nestling barn swallows, *Hirundo rustica*. *Animal Behaviour*, **66**, 1003–1010.

Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernardi, F., & Møller, A. P. 2000. Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 57–61.

Sankamethawee, W., Gale, G. A., & Hardesty, B. D. 2009. Post-fledgling survival of the cooperatively breeding puff-throated bulbul (*Alophoixus pallidus*). *Condor*, **111**, 675–683.

Santema, P., & Clutton-Brock, T. 2013. Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Animal Behaviour*, **85**, 655–661.

Schaller, G. B., & Emlen, S. T. 1961. The development of visual discrimination patterns in the crouching reactions of nestling grackles. *Auk*, **78**, 125–137.

Schiel, N., & Huber, L. 2006. Social influences on the development of foraging behavior in free-living common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, **68**, 1–11.

Schuett, G. W. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour*, **54**, 213–224.

Seyfarth, R. M., Cheney, D. L., & Marler, P. M. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, **28**, 1070–1094.

Sharp, S. P., & Hatchwell, B. J. 2005. Individuality in the contact calls of cooperatively breeding long-tailed tits (*Aegithalos caudatus*). *Behaviour*, **142**, 1559–1575.

Sharp, S. P., McGowan, A., Wood, M. J., & Hatchwell, B. J. 2005. Learned kin recognition cues in a social bird. *Nature*, **434**, 1127–1130.

Shizuka, D., & Lyon, B. E. 2013. Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism. *Ecology Letters*, **16**, 315–22.

Slocombe, K. E., & Zuberbühler, K. 2005. Functionally referential communication in a chimpanzee. *Current Biology*, **15**, 1779–1784.

Smiseth, P. T., Darwell, C. T., & Moore, A. J. 2003. Partial begging: an empirical model for the early evolution of offspring signalling. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1773–1777.

Smiseth, P. T., Kölliker, M., & Royle, N. J. 2012. What is parental care? In: *The Evolution of Parental Care*, (Ed. by N. J. Royle, P. T. Smiseth, & M. Kölliker), pp. 1–17. Oxford University Press.

Smiseth, P. T., & Moore, A. J. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Animal Behaviour*, **63**, 577–585.

Smiseth, P. T., & Moore, A. J. 2007. Signalling of hunger by senior and junior larvae in asynchronous broods of a burying beetle. *Animal Behaviour*, **74**, 699–705.

Smiseth, P. T., Wright, J., & Kölliker, M. 2008. Parent-offspring conflict and co-adaptation: behavioural ecology meets quantitative genetics. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1823–1830.

Smith, H. G., & Montgomerie, R. 1991. Nestling American robins compete with siblings by begging. *Behavioral Ecology and Sociobiology*, **29**, 307–312.

Spence, K. W. 1936. The nature of discrimination learning in animals. *Psychological Review*, **43**, 427–449.

Stacey, P. B., & Koenig, W. D. Eds. 1990. *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior.* Cambridge University Press.

Suedkamp Wells, K. M., Ryan, M. R., Millspaugh, J. J., Thompson III, F. R., & Hubbard, M. W. 2007. Survival of postfledgling grassland birds in Missouri. *Condor*, **109**, 781–794.

Sullivan, K. A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constaints. *Ecology*, **69**, 118–124.

Suzuki, T. N. 2011. Parental alarm calls warn nestlings about different predatory threats. *Current Biology*, **21**, R15–R16.

Symonds, M. R. E., & Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, **65**, 13–21.

Tabachnick, B. G., & Fidell, L. S. 2001. *Using Multivariate Statistics.* 4th edn. Boston, Massachusetts: Allyn and Bacon.

Taborsky, B. 2006. The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 741–750.

Tallamy, D. W. 1985. "Egg dumping" in lace bugs (*Gargaphia solani*, Hemiptera: Tingidae). *Behavioral Ecology and Sociobiology*, **17**, 357–362.

Tallamy, D. W., & Denno, R. F. 1981. Maternal care in *Gargaphia solani* (Hemiptera: Tingidae). *Animal Behaviour*, **29**, 771–778.

Tanaka, K. D., & Ueda, K. 2005. Horsfield's hawk-cuckoo nestlings simulate multiple gapes for begging. *Science*, **308**, 653.

Terkel, J. 1996. Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: *Social Learning in Animals: The Roots of Culture*, (Ed. by C. M. Heyes & B. G. Galef Jr.), pp. 17–47. San Diego, CA: Academic Press, Inc.

Thompson, A. M., & Ridley, A. R. 2013. Do fledglings choose wisely? An experimental investigation into social foraging behaviour. *Behavioral Ecology and Sociobiology*, **67**, 69–78.

Thornton, A. 2008a. Early body condition, time budgets and the acquisition of foraging skills in meerkats. *Animal Behaviour*, **75**, 951–962.

Thornton, A. 2008b. Social learning about novel foods in young meerkats. *Animal Behaviour*, **76**, 1411–1421.

Thornton, A., & Hodge, S. J. 2008. The development of foraging microhabitat preferences in meerkats. *Behavioral Ecology*, **20**, 103–110.

Thornton, A., & Malapert, A. 2009. The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1269–1276.

Thornton, A., & McAuliffe, K. 2006. Teaching in wild meerkats. *Science*, **313**, 227–229.

Thornton, A., & Raihani, N. J. 2008. The evolution of teaching. *Animal Behaviour*, **75**, 1823–1836.

Thorogood, R., Ewen, J. G., & Kilner, R. M. 2011. Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2638–2645.

Tibbetts, E. A., & Dale, J. 2007. Individual recognition: it is good to be different. *Trends in Ecology & Evolution*, **22**, 529–537.

Townsend, S. W., Allen, C., & Manser, M. B. 2012. A simple test of vocal individual recognition in wild meerkats. *Biology Letters*, **8**, 179–182.

Townsend, S. W., Zöttl, M., & Manser, M. B. 2011. All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behavioral Ecology and Sociobiology*, **65**, 1927–1934.

Träger, I., Masello, J. F., Mundry, R., & Quillfeldt, P. 2006. Do acoustic parameters of begging calls of Cory's shearwaters *Calonectris diomedea* reflect chick cody condition? *Waterbirds*, **29**, 315–206.

Trillmich, F., & Wolf, J. B. W. 2007. Parent–offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology*, **62**, 363–375.

Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist*, **14**, 249–264.

Valencia, J., De La Cruz, C., Carranza, J., & Mateos, C. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. *Animal Behaviour*, **71**, 1021–1028.

Verhulst, S., & Hut, R. A. 1996. Post-fledging care, multiple breeding and the costs of reproduction in the great tit. *Animal Behaviour*, **51**, 957–966.

Villaseñor, E., & Drummond, H. 2007. Honest begging in the blue-footed booby: signaling food deprivation and body condition. *Behavioral Ecology and Sociobiology*, **61**, 1133–1142.

Visalberghi, E., & Addessi, E. 2000. Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour*, **60**, 69–76.

Waelti, M. O., & Reyer, H.-U. 2007. Food supply modifies the trade-off between past and future reproduction in a sexual parasite-host system (Rana esculenta, Rana lessonae). *Oecologia*, **152**, 415–424.

Wagner, W. E. 1989. Fighting, assessment, and frequency alteration in Blanchard' s cricket frog. *Behavioral Ecology and Sociobiology*, **25**, 429–436.

Warburton, K. 2003. Learning of foraging skills by fish. *Fish and Fisheries*, **4**, 203–215.

Weary, D. M., & Fraser, D. 1995. Calling by domestic piglets: reliable signals of need? *Animal Behaviour*, **50**, 1047–1055.

Weygoldt, P. 1980. Complex brood care and reproductive behavior in captive poison-arrow frogs, *Dendrobates pumilio* O. Schmidt. *Behavioral Ecology and Sociobiology*, **7**, 329–332.

Wheelwright, N. T., & Templeton, J. J. 2003. Development of foraging skills and the transition to independence in juvenile savannah sparrows. *Condor*, **105**, 279–287.

Wiklund, C. G. 1990. Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. *Behavioral Ecology and Sociobiology*, **26**, 217–223.

Yasukawa, K., Urish, J., Her, A., & Light, E. 2008. Similarity in the begging calls of nestling Red-winged Blackbirds. *Journal of Field Ornithology*, **79**, 254–262.

Ydenberg, R., & Dill, L. M. 1986. The economics of fleeing from predators. In: *Advances in the Study of Behavior*, (Ed. by J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater), pp. 229–249. Academic Press, Inc.

Yoerg, S. I. 1994. Development of foraging behavior in the Eurasian dipper, *Cinclus cinclus*, from fledgling until dispersal. *Animal Behaviour*, **47**, 577–588.

Yoerg, S. I. 1998. Foraging behavior predicts age at independence in juvenile Eurasian dippers (*Cinclus cinclus*). *Behavioral Ecology*, **9**, 471–477.

Young, A. J., & Clutton-Brock, T. 2006. Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters*, **2**, 385–387.

Zahavi, A. 1975. Mate selection-a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–14.

Zahavi, A. 1977a. The cost of honesty. *Journal of Theoretical Biology*, **67**, 603–605.

Zahavi, A. 1977b. Reliability in communication systems and the evolution of altruism. In: *Evolutionary Ecology*, (Ed. by B. Stonhouse & C. Perrins), pp. 253–259. University Parks Press.

Zweifel, R. G. 1968. Effects of temperature, body size, and hybridization on mating calls of toads, Bufo a . americanus and Bufo woodhousii fowleri. *Coepia*, **1968**, 269–285.

References

Appendix 1 – Nestling v fledgling competition

A1.1 Methods

I used video recordings to quantify the level of competition that existed between nestling pied babblers. Video analysis was carried out using VLC 2.0.1 media player (VideoLAN Project, www.videolan.ord). All feeding events were scored for the number of nestlings begging to the provisioning adult. Begging was defined as gaping and posturing towards the provisioning bird. If more than one nestling was begging at the same provisioning adult then this was classified as a competitive solicitation interaction, if only one nestling was begging then this was classified as no-competitive. Nest cameras were placed at pied babbler nests during the nest building when the group was known to be foraging away from the nest, to avoid disturbance of fully active nests. Cameras were placed roughly 30 cm from the nest rim, above and to one side of the nest to maximize the view of the nest and provisioning events. A DVR was placed at the base of the nest tree, hidden from view using natural debris, and the cables connecting it to the camera were camouflaged. Nest cameras were Swann Security SpyCams SWSPY-DSC (Swann Communications Pty. Ltd., Port Melbourne, Australia) and the DVRs were Archos 405s (Archos Inc., Denver, USA). We recorded 1893 minutes of footage on nestlings whose age ranged from 7-12 days post-hatching.

I used the social foraging data from our *ad libitum* data collection (Altmann 1974) to investigate competition in fledgling pied babblers. Total social foraging time was calculated as the sum of each fledglings social foraging time. Competitive social foraging interactions were classified as those where two or more fledglings were socially foraging with the same adult. All competitive social foraging interactions were summed to give a total for competitive social foraging. Groups with only one fledgling were not included in these analyses.

A1.2 Results

There was a significant difference in the level of competition for feeds between the nestling and the fledgling phase (two-sample binomial test, $p<0.001$). The nestling phase was more

competitive than the fledgling phase: 85.4% of nestling feeds were competitive (276 out of 330 feeds), compared to 4.4% of fledgling feeds (48 out of 1087 feeds) (See figure A1).

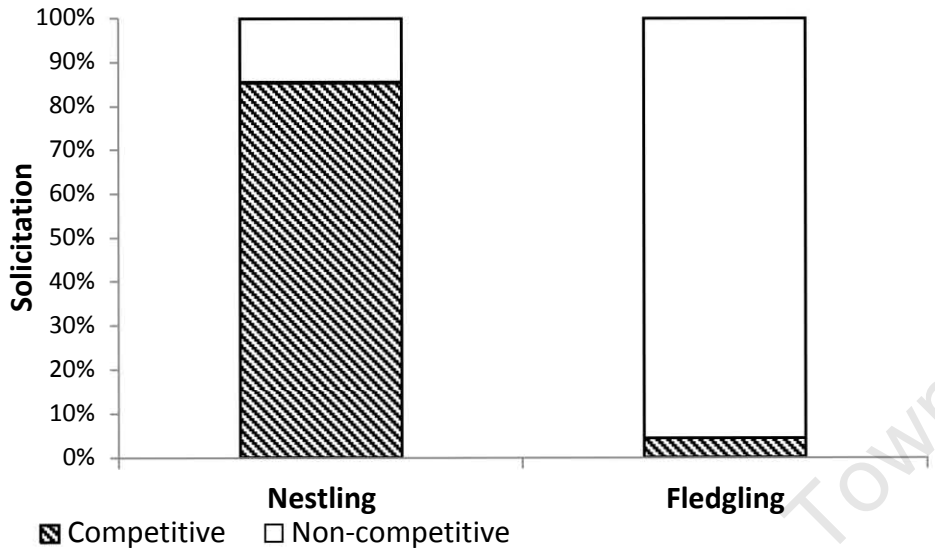

Figure A1 Graph showing the proportion of nestling and fledgling solicitation events that were competitive or non-competitive. Nestling solicitation events were feeding events at the nest, while fledgling solicitation events were social-foraging interactions between fledglings and adult care-givers.